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Functional diversity enhances detection of ecosystem stability and resolution of predator-prey interactions within a multitrophic community

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FUNCTIONAL DIVERSITY ENHANCES DETECTION OF ECOSYSTEM STABILITY AND RESOLUTION OF PREDATOR-PREY INTERACTIONS WITHIN A MULTITROPHIC COMMUNITY

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"In the loving memory of my father, Bert A. Kissick, who fostered my childhood interest in nature and encouraged my pursuit of a career in science."

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TABLE OF CONTENTS

Page
LIST OF TABLES x
LIST OF FIGURES xiii
ABSTRACT xx
CHAPTER 1. INTRODUCTION 1
1.1 Introduction 1
1.2 Functional diversity 3
1.3 Functional insurance and ecological stability mechanisms 4
1.4 Landscape scale response 6
1.5 Avian vision 7
1.6 Linking trophic levels with prey visual contrasts 10
1.7 Ecological significance of the Cerambycidae 12
1.8 Ecological significance of the beetles that depredate wood-borers 14
1.9 Effects of habitat loss and fragmentation on species 15
1.10 Bibliography 17

CHAPTER 2. MECHANISMS OF BIRD VISION AND CURRENT METHODS FOR STUDYING VISION-MEDIATED AVIAN BEHAVIOR WITH EMPHASIS ON INSECT PREY 29
2.1 Introduction 29
2.2 Differences between human and avian vision 31
2.2.1 Anatomical differences between human and avian eyes 31
2.2.2 The retina 35
2.2.2.1 Spectral range and photoreceptor types 36
2.2.2.2 Oil droplets function as an ocular filter 40
2.3 Predictions of spectral tuning of the SWS1 cone type 41
2.4 Modeling avian tetrachromatic color space 43
2.5 Significance of UV vision on avian behavior 50
2.6 Conclusions 53
2.7 Bibliography 55

CHAPTER 3. NOVEL FUNCTIONAL TRAITS CAPTURE THE FUNCTIONAL SPECTRUM OF SPECIES AND DETECT CHANGES IN ECOSYSTEM STABILITY ALONG ENVIRONMENTAL GRADIENTS 64
3.1 Introduction 64

Page

3.2 Materials and Methods 70
3.2.1 Beetle collection 70
3.2.2 Landscape data (#1 in Fig. 3.3) 72
3.2.3 Functional traits (Table 3.1, #1 – 3 in Fig. 3.4) 73
3.2.4 Functional groupings (#4 in Fig. 3.4) 78
3.2.5 Gradient analysis (Figure 3.3) 79
3.2.5.1 Community (RDA, #2 in Fig. 3.3) 80
3.2.5.2 Three dimensional surface of functional richness (#3 in Fig. 3.3) 80
3.2.5.3 Functional groups (#4 – 5 in Fig. 3.3) 81
3.2.5.4 Threshold response (#6 in Fig. 3.3) 83
3.3 Results 84
3.3.1 Functional groupings (Figure 3.5) 84
3.3.2 Community (RDA analyses, triplots shown in Appendices J and K 84
3.3.2.1 3D surface of functional richness (Fig. 3.6) 86
3.3.3 Functional groups (Fig. 3.7, Appendix I) 86
3.3.4 Threshold response (Table 3.2, Fig. 3.8) 88
3.3.5 General comments 91
3.4 Discussion 91
3.4.1 Conclusions 97
3.5 Bibliography 99

CHAPTER 4. MECHANISMS OF ECOLOGICAL STABILITY DETECTED IN A MULTITROPHIC COMMUNITY 110
4.1 Introduction 110
4.2 Materials and Methods 116
4.2.1 Beetle sampling and functional groups 116
4.2.2 Landscape assessment 117
4.2.3 Ecosystem stability mechanisms 118
4.2.3.1 Cross-scale resilience (Fig. 4.2, I) 118
4.2.3.2 Response diversity (Fig. 4.2, II) 119
4.2.3.3 Density compensation (Fig. 4.2, III) 120
4.3 Results 122
4.4 Discussion 125
4.5 Bibliography 132

CHAPTER 5. CHANGES IN COMMUNITY STRUCTURE ARE LINKED TO VISION-MEDIATED PREDATOR-PREY INTERACTIONS 141
5.1 Introduction 141
5.2 Materials and Methods 148
5.2.1 Beetle and bird collection 148
5.2.2 Beetle visual contrasts 149
5.2.3 Beetle visual contrast groups 152
5.2.4 Avian assemblages (Appendix N) 153

Page
5.2.5 Analysis 153
5.3 Results 154
5.4 Discussion 160
5.5 Bibliography 167

CHAPTER 6. CONCLUSIONS 178
6.1 Conclusion 178
6.2 Bibliography 188

APPENDICES
Appendix A: Functional traits obtained for predator beetles (Coleoptera: Cleridae, Cucujidae, Histeridae, Passandridae) and literature cited for wood-borer and predator functional traits 189
Appendix B: Functional traits obtained for wood-boring beetles (Coleoptera: Cerambycidae) 221
Appendix C: Landscape metrics calculated at each of the 12 analytical foci (90 m – 7.29 km) 232
Appendix D: Methods to assess the avian visual perception functional trait 234
Appendix E: Backgrounds used in chromatic and achromatic contrasts used in avian visual perception functional trait categorization 240
Appendix F: Colorimetric variables for use in the avian visual perception functional trait categorization 242
Appendix G: Standardized coefficients from multiple regression of functional redundancy (FR) and response diversity (RD) of each functional group (FG) with fragmentation 244
Appendix H: Proportion of variance explained by models (redundancy analysis (RDA) and multiple regression 254
Appendix I: Dendrograms of wood-boring beetle (Coleoptera: Cerambycidae) and predator beetle functional groupings 256
Appendix J: Redundancy analysis (RDA) triplots of wood-boring beetle functional diversity indices (FDiv, FEve, and FRic) with landscape. Only the significant relationships are given 261
Appendix K: Redundancy analysis (RDA) triplots of predator beetle functional diversityindices (FDis, FDiv, FEve, and FRic) with landscape. Only the significant relationships are given 268
Appendix L: Backgrounds used in chromatic and chromatic contrast calculations in Chapter 5 274
Appendix M: Members of beetle visual contrast groups 276
Appendix N: Members of avian assemblages 278
Appendix O: Beetles collected among field sites (Chapter 5) 283
Appendix P: Birds collected among field sites 285

VITA 286

LIST OF TABLES

Table Page

Table 2.1 Summary of the most significant anatomical differences between human and diurnal, insectivore bird eyes 30

Table 3.1 Functional traits selected to capture the functional spectrum of beetles in hardwood forests. Traits were obtained from literature, directly measured (M) or calculated (C). New traits developed here include "landscape response trend" and "avian visual perception." 74

Table 3.2 Best model selection (in bold) for wood-borer and predators at the community and functional group levels. "NA" for FGA signifies that the segmented model examined at a focus of 0.81 km did not have the lowest AIC score 89

Table 3.3 Number of species (functional redundancy) within each functional group. Species cannot be classified within multiple functional groups 94

Table 4.1 Longhorned beetle and predator functional groups, the major traits that discriminate them, and the number of species they contain. Species are only found in a single functional group 117

Table 4.2 Contingency table containing the number of species within each functional group that have the same landscape response trend..... 123

Table 4.3 Significance of the interaction terms from the quasi-Poisson generalized linear models indicating the presence of response diversity within each beetle functional group 124

Appendix Table

Table A.1 Cerambycid functional traits subfamily, tribe, mean size, landscape response, avian visual perception 189

Table A.2 Abbreviations for Table 1 and literature cited for Tribe and Subfamily 193

Appendix Table Page

Table A.3 Cerambycid functional traits Hymenoptera resemblance, diel activity, host range, host genera, host family. Blank entries indicate missing values 194

Table A.4 Abbreviations for Table 3 and literature cited for Hymenoptera resemblance, diel activity, host family, and host genera 198

Table A.5 Cerambycid functional traits host condition, larval wood type, adult feeding behavior, plant part attacked (larvae) 200

Table A.6 Abbreviations for Table5 and literature cited for host condition, larval wood type, adult feeding behavior, and plant part attacked (larvae) 204

Table A.7 Cerambycid functional traits, plant layer attacked (larvae) flight period 206

Table A.8 Abbreviations for Table7 and literature cited for flight period 209

Table A.9 Cerambycid functional traits, host family 210

Table A.10 Abbreviations for table 9, literature cited for host family 214

Table B.1 Predator functional traits, subfamily, mean size (mm), body form, resemblance, and avian visual perception 221

Table B.2 Abbreviations for Table 1, literature cited for Subfamily, body form, and resemblance 223

Table B.3 Predator functional traits landscape response, diel activity, flight activity, tree type, and tree state 224

Table B.4 Abbreviations for Table 3, literature cited for diel activity, flight activity, tree type, and tree state 226

Table B.5 Table 5: Predator functional traits larval feeding, larval habitat, adult feeding, and adult habitat 227

Table B.6 Abbreviations for Table 3, literature cited for larval feeding, larval habitat, adult feeding, and adult habitat 229

Table C.1 Radius of each analytical focus. Radii retained in analysis are highlighted in gray 233

Table E.1 Hymenoptera species whose reflectance was measured for the avian visual perception functional trait categorization 240

Appendix Table Page

Table E.2 Common forest substrates whose reflectance was measured for the avian visual perception trait categorization 241

Table F.1 Colorimetric variables (23 total) calculated for beetles with R package "pavo" for use in the avian visual perception functional trait categorization. Abbreviations for each colorimetric variable are also given 242

Table H.1 Proportion of variance explained by model (proportion explained by constrained axes (RDA) or R-squared value (multiple regression). Selected spatial foci are highlighted in gray 254

Table H.2 Landscape focus and landscape metrics selected for threshold analyses at the community and functional group levels 255

Table L.1 Backgrounds used in chromatic and achromatic contrast calculations in Chapter 5 274

Table N.1 Members of avian assemblages including scientific name, family, feeding guild and estimated cone type 278

Table O.1 Beetles collected among field sites for Chapter 5. Removed species with <=5 total individuals among sites (in gray) 283

Table P.1 Birds collected among field sites. Removed species with <=10 total individuals among sites (in gray) 285

LIST OF FIGURES

Figure Page

Figure 2.1 Diagrams of human and avian eyes to show the anatomical differences between them. A. Human eye, adapted from Junqueira & Carneiro (2003). B. Avian eye, adapted from Rowe (2000) 32

Figure 2.2 The avian retina in an area approaching the fovea to illustrate its cell layers including the photoreceptor layer. The choroid contains pigmented epithelium to prevent the reflection of light not initially absorbed by the photoreceptors. Adapted from a figure illustrating the human retina in (Junqueira & Carneiro 2003) 35

Figure 2.3 Spectral sensitivities of the avian retina (given in probability of absorption) and the human retina (given in relative absorption). "UV" and "V" indicate the spectral sensitivities of the SWS1 (short wave sensitive) cones. S = short wave sensitive; M = medium wave sensitive; L = long wave sensitive. The avian retina spectral sensitivities were adapted from Endler & Mielke (2005). The human retinal spectral sensitivities were adapted from Goldsmith (1990)..... 38

Figure 2.4 Avian rods and cones including four single cones (one being either UV- or V-sensitive), double cones, and rods. The oil droplets of cones are also shown to illustrate their position in the distal portion of the cone's inner segment and their pigmentation type. Adapted from Toomey et al. (2015) 39

Figure 2.5 Hypothetical depiction of the visual contrast between *Cucujus clavipes*, a predator beetle, and a maple leaf, *Acer saccharum*, under full sunlight within avian tetrahedral color space of the yellow-billed cuckoo, *Coccyzus americanus*. V = violet-sensitive photoreceptor; R = red-sensitive photoreceptor; G = green-sensitive photoreceptor; B = blue-sensitive photoreceptor; ΔS = chromatic contrast 44

Figure 3.1 Two-dimensional representations of functional diversity indices. FEve, FRic, and FDiv were adapted from Villéger et al. (2008). FDis was adapted from Laliberté & Legendré (2010) 67

Figure 3.2 Field sites selected along a gradient of forest fragmentation in the state of Indiana, USA..... 71

Figure Page

Figure 3.3 Flowchart outlining methods to assess changes in functional diversity along the fragmentation gradient. I examined how functional diversity changed, including whether functional diversity displayed a threshold change, along the gradient at community and functional group levels 76

Figure 3.4 Flowchart outlining methods to obtain functional groupings of beetles. Methods include the collection of all functional traits used to categorize wood-borer and predator beetles into functional groups 77

Figure 3.5 Dendrogram depicting three wood-borer functional groups and two predator functional groups. Icons represent discriminating traits that were present in >50% of the species within the functional group 85

Figure 3.6 Three-dimensional curves that represent change in functional richness (FRic) of beetle communities along two aspects of landscape pattern, patch interspersion (landscape division index, LDI) and patch shape complexity (mean shape index, MSI). A. Wood-borer FRic. B. Predator FRic. C. Community FRic 87

Figure 3.7 The relationship of functional redundancy (FR) and response diversity (RD) of wood-borer and predator functional groups with fragmentation..... 88

Figure 3.8 Threshold responses of predator community functional dispersion (FDis) to total area ($p = 0.0397$) and functional redundancy (FR) of predator FGB to mean shape index ($p = 0.00458$) 90

Figure 4.1 Three proposed stability mechanisms related to the functional insurance hypothesis. These mechanisms provide ecosystem resilience through the asynchronous responses of species with similar ecological function 112

Figure 4.2 Flowchart depicting methods used to detect the three proposed stability mechanisms: cross-scale resilience, response diversity, and density compensation 121

Figure 4.3 Six landscape response trends generated from loess smoothing of |rho| vs. analytical focus of each beetle species grouped by Ward's clustering 122

Figure 4.4 Frequency distributions of Pearson's *r* to visualize presence of density compensation (negative covariance between species) within each functional group. Whether there were more negative than positive correlations between species within each functional group was tested with Wilcoxon signed rank tests (*p*-values are given in bold) 125

Figure Page

Figure 5.1 Hypothetical depiction of the visual contrast between *Cucujus clavipes*, a predator beetle, and a maple leaf, *Acer saccharum*, under full sunlight within avian tetrahedral color space of the yellow-billed cuckoo, *Coccyzus americanus*. V = violet-sensitive photoreceptor; R = red-sensitive photoreceptor; G = green-sensitive photoreceptor; B = blue-sensitive photoreceptor; ΔS = chromatic contrast 144

Figure 5.2 My predictions of vision-mediated interactions between birds and beetles. I predicted significant (S) correlations between the abundance of birds that glean substrates and the abundance of beetles that are not "cryptic" (similar to forest backgrounds) and not "aposematic" (similar to a wasp). *All other relationships are given a status of "nonsignificance (NS)" as a default 147

Figure 5.3 Flowchart illustrating methods to obtain visual contrast groups. Chromatic (dS) and achromatic (dL) contrasts were made between ninety-six beetle species and 1) five wasp species and 2) five forest substrates (top and bottom of leaves, bark, lichen, moss). These contrasts were calculated under three forest light conditions (closed canopy, small gap, and large gap) and two average avian visual systems, violet-sensitive (VS) and ultra-violet sensitive (UVS) 152

Figure 5.4 Beetle visual contrast groups (under ultraviolet-sensitive (UVS) and violet-sensitive (VS) bird models). Groups are defined by chromatic (dS) and achromatic (dL) contrasts with substrates. The direction of the arrows indicates whether the beetle has high or low contrast with substrates. Groups with double arrows have very high dS or dL values 155

Figure 5.5 Summary of results. I predicted significant (S) correlations between the abundance of birds that glean substrates and the abundance of beetles that are not "cryptic" (similar to forest backgrounds) and not "aposematic" (similar to a wasp). *All other relationships are given a status of "nonsignificance (NS)" as a default. My predictions were supported with substrate-gleaning birds with a violet-sensitive (VS) visual system but not for substrate-gleaning birds with an ultraviolet-sensitive (UVS) visual system 156

Figure 5.6 Example of a redundancy analysis (RDA) triplot. This is one example of 18 bird-beetle triplots. This plot shows beetle visual contrast group 3 (under a VS bird model, thus VS.3) and birds (with estimated violet-sensitive (VS) vision) that glean bark 157

Figure 5.7 Example of a redundancy analysis (RDA) triplot. This is one example of 18 bird-beetle triplots. This plot shows beetle visual contrast group 3 (under a VS bird model, thus VS.3) and birds (with estimated violet-sensitive (VS) vision) that glean leaves 158

Figure Page

Figure 5.8 Example of a redundancy analysis (RDA) triplot. This is one example of 18 bird-beetle triplots. This plot shows beetle visual contrast group 4 (under a VS bird model, thus VS.4) and birds (with estimated violet-sensitive (VS) vision) that flycatch..... 159

Figure 5.9 Reflectance spectra of A) *Aegomorphus modestus* and B) *Gaurotes cyanipennis*, two visually apparent beetles to birds regardless of avian visual system 163

Appendix Figure

Figure G.1 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG1 functional redundancy. Variable 1: aggregation index, mean patch area, proportion landscape, or total area; Variable 2: edge density, landscape division index, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index 244

Figure G.2 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG1 response diversity. Variable 1: aggregation index or total area; Variable 2: edge density, landscape division index, landscape shape index, mean fractal dimension index, mean shape index 245

Figure G.3 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG2 functional redundancy. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, or mean shape index 246

Figure G.4 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG2 response diversity. Variable 1: aggregation index, mean patch area, proportion landscape, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean shape index 247

Figure G.5 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG3 functional redundancy. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index..... 248

Figure G.6 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG3 response diversity. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index..... 249

Appendix Figure Page

Figure G.7 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGA functional redundancy. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, mean fractal dimension index, mean perimeter area ratio, mean shape index 250

Figure G.8 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGA response diversity. Variable 1: aggregation index, mean patch area, proportion landscape, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, or mean shape index 251

Figure G.9 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGB functional redundancy. Variable 1: aggregation index, proportion landscape, or total area; Variable 2: edge density, landscape division index, mean fractal dimension index, mean shape index, or total edge..... 252

Figure G.10 Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGB response diversity. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index 253

Figure I.1 Dendrogram of wood-boring beetle functional groups 256

Figure I.2 Branch of wood-boring beetle functional group 1 (FG1) 257

Figure I.3 Branch of wood-boring beetle functional group 2 (FG2) 258

Figure I.4 Branch of wood-boring beetle functional group 3 (FG3) 259

Figure I.5 Dendrogram of predator beetle functional groups 260

Figure J.1 Redundancy analysis (RDA) triplot at an analytical focus of 0.81 km (Focus 6). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 261

Figure J.2 Redundancy analysis (RDA) triplot at an analytical focus of 1.35 km (Focus 7). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 262

Appendix Figure Page

Figure J.3 Redundancy analysis (RDA) triplot at an analytical focus of 1.89 km (Focus 8). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 263

Figure J.4 Redundancy analysis (RDA) triplot at an analytical focus of 2.43 km (Focus 9). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 264

Figure J.5 Redundancy analysis (RDA) triplot at an analytical focus of 4.05 km (Focus 10). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 265

Figure J.6 Redundancy analysis (RDA) triplot at an analytical focus of 5.67 km (Focus 11). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 266

Figure J.7 Redundancy analysis (RDA) triplot at an analytical focus of 7.29 km (Focus 12). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 267

Figure K.1 Redundancy analysis (RDA) triplot at an analytical focus of 0.81 km (Focus 6). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 268

Figure K.2 Redundancy analysis (RDA) triplot at an analytical focus of 1.35 km (Focus 7). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 269

Appendix Figure Page

Figure K.3 Redundancy analysis (RDA) triplot at an analytical focus of 1.89 km (Focus 8). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 270

Figure K.4 Redundancy analysis (RDA) triplot at an analytical focus of 2.43 km (Focus 9). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 271

Figure K.5 Redundancy analysis (RDA) triplot at an analytical focus of 5.67 km (Focus 11). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 272

Figure K.6 Redundancy analysis (RDA) triplot at an analytical focus of 7.29 km (Focus 12). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness 273

Figure M.1 Contrast groups using average avian UVS model in R package "pavo". Gray highlights = species retained in analysis 276

Figure M.2 Contrast groups (VS.1, VS.2, VS.3, and VS.4) using average avian VS model in R package "pavo". Gray highlights = species retained in analysis..... 277

ABSTRACT

Kissick, Ashley L. Ph.D., Purdue University, December 2016. Functional Diversity Enhances Detection of Ecosystem Stability and Resolution of Predator-Prey Interactions Within a Multitrophic Community. Major Professor: Jeffrey D. Holland.

Habitat fragmentation and loss are principal factors that contribute to the decline of biodiversity which in turn has a negative impact on ecosystem function. There has been growing interest in understanding diversity's role in the mechanisms behind ecosystem resilience with much attention focusing on how functional diversity, or the range of species' ecological roles in a community, impacts ecosystem function. Under the functional insurance hypothesis, stability in ecosystems is maintained by species that perform similar functions but have asynchronous responses to disturbance. There are three proposed stability mechanisms that operate through species' asynchronous responses: cross-scale resilience, response diversity, and density compensation. My objective in this study was to examine change in functional diversity resulting from habitat fragmentation and detect ecological stability mechanisms in a multitrophic community consisting of longhorned beetles and their beetle predators. I also considered predator-prey interactions between beetles and their insectivore avian predators at the community level.

To meet my objectives, I developed new functional traits to further capture beetle species' functional roles and new methodology for examining change in functional diversity across trophic levels. I also expanded methodology to better detect one ecological stability mechanism, cross-scale resilience. Here, cross-scale resilience was operating if species with similar function also had different landscape response trends. I also determined a new way to assess predator-prey interactions in a multitrophic community with the use of avian visual perception of beetle prey visual contrasts. This approach allowed me to directly examine changes in avian predator and beetle prey abundance.

I found that prey functional diversity was more negatively impacted than predator functional diversity by habitat fragmentation. I detected two ecological stability mechanisms, cross-scale resilience and response diversity, which may have provided the beetle community greater resilience to habitat fragmentation. With respect to the interactions between avian predators and beetle prey, variations in visual contrasts of beetles moderated the degree to which abundance of birds in some functional groups impacted beetle abundance. Also a "functional link" may also be important for providing a greater resolution between the relationships between predator and prey abundance. I suggest that future studies investigate how vision-mediated predator-prey interactions may simultaneously impact the functional diversity of these trophic levels. In addition, assessing three-dimensional surfaces of functional diversity could reveal best landscapes for promoting functional diversity of ecosystem service providers in local landscapes.

CHAPTER 1. INTRODUCTION

1.1 Introduction

Habitat fragmentation and loss are primary contributing factors to the decline of biodiversity. There is empirical evidence that species loss affects ecosystem function including processes like pollination, nutrient cycling, and seed dispersal. But in many cases it is the identity of the lost species that ultimately determines the extent of change that may occur after a disturbance event. Considering that human activity is dependent on ecosystems, attention has shifted to studying diversity's role in the mechanisms behind ecosystem resilience. Functional diversity is the range of species' ecological roles in a community. It has been proposed that functional diversity stabilizes ecosystems through functional redundancy and functional insurance (Díaz & Cabido 2001). Functional redundant communities are more resilient because if a species is lost from a community other species with similar functional roles are able to compensate for the loss (Walker 1992). In addition, species with similar functional roles having different response to disturbance provide insurance against the loss of function from the community (Johnson et al. 1996; Yachi & Loreau 1999).

In this research project I focused on assessing how habitat fragmentation impacts change in functional diversity of a multitrophic community and detecting ecological stability mechanisms operating in this community. Considering that birds are important

predators of beetles, I also developed methodology to link predator and prey trophic levels to examine how avian predators impact beetle abundance. My system of choice included longhorned beetles and their beetle predators due to their diverse ecological roles in temperate hardwood forests. I first expanded current methodology to establish functional groups of the beetles. To do this, I incorporated two new functional traits. One, landscape response, provided insight on species' dispersal, population dynamics, and foraging behavior. Another, avian visual perception of prey, incorporated predator-prey interactions into functional trait space. Both of these functional traits are inherent characteristics of species that further define species' functional roles in the community. I also used numerous other traits in addition to these two new traits to capture the functional spectrum of beetle species. These functional groupings were used to examine how functional diversity of a multitrophic community simultaneously changed along a habitat fragmentation gradient. I also examined the asynchronous response of species within these functional groups to detect underlining stability mechanisms operating in the community. In the process I developed new methodology to better identify one stability mechanism, cross-scale resilience. This involved using landscape response of species to landscape pattern across the entire range of ecologically important foci. I also expanded the avian visual perception prey trait to link beetle and bird trophic levels in order to examine the interplay between predator and prey abundances. This research study is the first to examine predator and prey abundances in this manner. I found that species' functional roles were also important for examining predator-prey interactions since the link between trophic levels had greater resolution when also incorporating a function link

(e.g., comparing abundances of beetles found in deadwood with abundances of birds that forage for insects in deadwood).

1.2 Functional diversity

Habitat fragmentation negatively impacts ecosystem function (Didham et al. 1996, Haddad et al. 2015). Functional diversity, "the range and value of those species and organismal traits that influence ecosystem functioning" (Tilman 2001) may correlate better with ecosystem processes than species diversity after disturbance (Tilman et al. 1997, Díaz & Cabido 2001, Heemsbergen et al. 2004, Dang et al. 2005, Ernst et al. 2006, Scherer-Lorenzen 2008). Functional diversity may provide resilience of communities to disturbance through functional redundancy and functional insurance (Díaz & Cabido 2001). The functional redundancy hypothesis states that after an extirpation event in a community, species with similar roles as the lost species are able to compensate for the loss (Walker 1992). In addition, the functional insurance hypothesis states that stability in ecosystems is maintained by species performing similar functions but having different responses to disturbance (Johnson et al. 1996, Yachi & Loreau 1999). Overall, community resilience is achieved by communities containing functionally redundant species providing insurance against species loss by having variable responses to disturbance.

Investigations of changes in functional diversity along environmental gradients (de Bello et al. 2005) and with habitat degradation (Villéger et al. 2010) have led to to the development of indices that measure various features of functional trait space (e.g., Walker et al. 1999, Petchey & Gaston 2002, Villéger et al. 2008, Laliberté & Legendre

2010). Mason et al. (2005) identified that functional diversity can be described by functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv); while Laliberté and Legendre (2010) identified a fourth index, functional dispersion (FDis). These concepts were later developed into multidimensional indices to measure changes in functional diversity (Villéger et al. 2008, Laliberté & Legendre 2010). Overall, these indices measure the diversity of species' functional roles within multidimensional trait space and how species abundance is dispersed within this trait space. FRic represents the volume of trait space, FEve describes how even species abundance is distributed within trait space, FDiv measures how species abundance is spread along the range of the functional trait axis, and FDis is the mean distance of species to the centroid where the centroid is weighted towards the most abundant species. These indices are better predictors of ecosystem function than species richness and abundance (Gagic et al. 2015).

I thus examine changes in functional diversity of longhorned beetles and their beetle predators along gradients of forest loss and fragmentation. Functional diversity is examined at the community level using the four functional diversity indices proposed by Villéger et al. (2008) and Laliberté et al. (2010). Changes in response diversity, measured by FDis at the functional group level (Laliberté et al. 2010), and functional redundancy is examined at the functional group level.

1.3 Functional insurance and ecological stability mechanisms

The functional insurance hypothesis states that stability in ecosystems is maintained through the asynchronous responses of functionally similar species to

disturbance (Johnson et al. 1996, Yachi & Loreau 1999). Under the hypothesis, an increased number of species with similar functional roles but different temporal responses buffer communities from environmental change. The functional insurance hypothesis has been supported by both theoretical modeling (Yachi & Loreau 1999) and controlled experiments (Naeem & Li 1997, Leary & Petchy 2009).

There are three mechanisms through which ecosystems may be stabilized by asynchronous response of species: density compensation (Naeem & Li 1997), response diversity (Chapin III et al. 1997, Walker et al. 1999, Elmqvist et al. 2003, Nyström 2006, Chillo et al. 2011), and cross-scale resilience (Peterson et al. 1998, Steffan-Dewenter et al. 2002). Density compensation occurs when the decrease in abundance of one species is followed by an increase in the abundance of another species (Naeem & Li 1997) whereas response diversity is said to occur when an environmental change causes populations of some species to increase while causing other populations to decrease (Chapin III et al. 1997, Walker et al. 1999). Cross-scale resilience occurs when species with similar ecological roles respond to the landscape at different spatial scales (Peterson et al. 1998, Steffan-Dewenter et al. 2002). Support has been found for these mechanisms in diverse systems (McGrady-Steed & Morin 2000, Li et al. 2006, Winfree & Kremen 2009, Longino & Colwell 2011). I identify which of these stability mechanisms are operating within the functional groups of longhorned beetles and their predators to further test the functional insurance hypothesis. In the process, I propose new methodology to detect cross-scale resilience in communities.

1.4 Landscape scale response

Species, including longhorned beetles, respond to landscape patterns at different analytical foci (Holland et al. 2004, Yang 2010). Here, I refer to analytical foci (hearafter called "foci") as the distance, or the radius of measurement of landscape patterns, which is used as a predictor of species response. The best focus of species' landscape response can be determined by assessing landscape pattern at different foci and using these to predict species abundance. The model with the most explanatory power indicates the appropriate focus to assess the relationship of species abundance with landscape pattern (Holland et al. 2005).

The focus at which individuals respond to landscape pattern may be influenced by dispersal, population dynamics, foraging behavior, among other processes (Addicott et al. 1987, Dunning et al. 1992). With respect to active dispersal, there is a positive correlation between body size and dispersal ability (Jenkins et al. 2007). Beetles with larger body size responded to the landscape at a larger focus, thus body size may also be a contributing factor to the dispersal of longhorned beetles (Holland et al. 2005). Furthermore, if a species utilizes complimentary habitats, it may respond to the landscape at larger foci than species that specialize on a particular habitat (Addicott et al. 1987).

Species' landscape response may therefore be an inherent characteristic of a species (Holland et al. 2005), so I aimed to add this as another dimension of species' functional trait space. Importantly, this incorporates individuals' movement which determines how they interact with their environment (e.g.., dispersal and foraging range). Furthermore, if one ecological stability mechanism, cross-scale resilience, is operating in communities, species with similar functional roles that respond to the landscape at

different foci contribute to the resilience of communities after disturbance (Peterson et al. 1998, Steffan-Dewenter et al. 2002). Previous studies only consider the single best explanatory focus rather than species' response across multiple foci to determine whether species respond to the landscape differntly. However, I propose new methodology to assess landscape scale response as both a functional trait and an indicator for cross-scale resilience using species' response across all ecologically relevant foci.

1.5 Avian vision

Birds are important predators of beetles in temperate forests (The Birds of North America N.D.), and vision is used by birds to detect their prey. However, considering that many beetles display warning or cryptic signals to their avian predators, avian vision can be considered as a functional link between avian predators and beetle prey. Studies of avian vision have demonstrated that the avian eye is capable of vision that surpasses that of a human (Chapter 2). There are specific distinctions between the human and avian retina which contribute to the differences in vision between these animals. Considering that these differences exist, human vision is not relevant for evaluating prey's visual appearance to a bird. Therefore, we must take into account avian visual perception to remove any human bias.

One main distinction is that birds have a wider visual spectrum than humans. Whereas the human retina contains rods and three types of cones, the avian retina contains rods, double cones, and four types of single cones (Cuthill 2006). Cones are used in photopic vision (vision used under well-lit conditions) (Hart 2001) whereas rods are used in scotopic (or dark-adapted) vision (Wyszecki & Stiles 1982, pp. 252). Double

cones are used to detect brightness (Jones & Osorio 2004). Campenhausen and Kirschfeld thought they are used in motion as well (as cited in Hart 2001). The four single cones of the avian retina each have a different photopigment that is sensitive to distinct wavelengths of light: 1) SWS1 (cone with short-wave sensitivity to either violet or ultraviolet (UV) wavelengths (405 – 420 nm, or 355 – 370 nm, respectively)), 2) SWS2 (cone with short-wave sensitivity to blue wavelengths (~430 – 460 nm)), 3) MWS (cone with medium-wave sensitivity to green wavelengths (~505 nm)), and 4) LWS (cone with long-wave sensitivity to red wavelengths (~565 nm)) (Cuthill 2006). These four cone types contribute to birds having tetrachromatic color vision. Humans, however, are trichromats having just three single cones with photopigment sensitivity at red (LWS, 560 nm), green (MWS, 530 nm) (Schnapf et al. 1987) and blue (SWS1, ~ 420 nm) (Dartnall et al. 1983) wavelengths. The short-wave sensitive cone in humans has some UV sensitivity, but since the ocular media between the lens and the retina is not transparent to wavelengths below 400 nm, humans are blind to UV light (Bennett & Cuthill 1994). Furthermore, birds have a more intense perception of color than humans do. The single cones of the avian retina contain oil droplets in the distal portion of the inner segment (Cuthill 2006). These oil droplets contain various concentrations and types of carotenoid pigments which act as ocular filters to certain wavelengths of light (Hunt et al. 2009). This serves to improve color discrimination (Vorobyev 2003).

Considering these differences in bird and human vision, it is inappropriate to consider how a prey item appears to a non-human predator under the confines of human vision. To circumvent this problem, models that incorporate physiological properties of the viewer's retina and spectroradiometry have been developed. Specifically, the model

proposed by Vorobyev et al. (1998) considers 1) the properties of the retina determined through microspectrophotometry, 2) the reflectance of two objects viewed by the perceiver, and 3) the environmental light conditions under which the two objects are viewed. The model plots the objects in the vision space of the viewer based on the stimulation of the viewer's photoreceptors. Considering that birds are tetrachromats, their vision space can be described by a three-dimensional tetrahedron, the edges of which are the sensitivities of the four different photoreceptors. The distance between the objects in tetrachromatic vision space represents the visual contrast between the two objects. How similar or disparate in appearance the objects are to the avian viewer is determined by whether the distance surpasses a critical threshold value.

This model relies on specific physiological properties of a bird's retina which may be determined through microspectrophotometry. However, this method involves acquiring live specimens, sacrificing them after being held under certain conditions, and dissecting their eyes to acquire spectral sensitivities of the photoreceptors in their retina (methods described in Hart et al. 1998, difficulties of sample preparation given in Carlson 1972). This complicated process is not always pragmatic for researchers, but molecular studies have provided an alternative method to estimate avian SWS1 cone type. The difference in violet-sensitive (VS) vs. UV-sensitive (UVS) spectral tuning is attributed to a single amino acid change in the SWS1 polypeptide (Wilkie et al. 2000, Yokoyama et al. 2000). Various studies have sequenced this region of the SWS1 gene from species for which microspectrophotometry data are available and have determined that this method accurately predicts SWS1 spectral tuning in birds (Ödeen et al. 2009). This approach has determined spectral tuning of species in numerous families across multiple orders (Ödeen

& Håstad 2003, Ödeen et al. 2011) allowing spectral tuning of birds to be estimated with phylogeny.

1.6 Linking trophic levels with prey visual contrasts

Since the development of the tetrachromatic vision model, much has been learned about vision-mediated predator-prey interactions with avian predators. Visual contrasts of insect prey can serve as a signal to avian predators (Cuthill et al. 2000), however the predator's response to the signal is variable (Lyytinen et al. 2004, Stobbe & Schaefer 2008, Olofsson et al. 2010). Specific to beetles considered here, the longhorned beetles and their beetle predators (at least to the human eye) have diverse color patterns that range from solid black to mottled gray to bright, contrasting colors, and some species are very similar to Hymenoptera in both appearance and behavior (Linsley 1959, Mawdsley 1994). Since birds also have spectral sensitivity at longer wavelengths, we can expect that these signals are also important for them (Lindstedt et al. 2011), but considering many species can visually detect UV, we must also consider the pattern under short wavelengths (Remington 1973). Here I consider whether these patterns are cryptic or aposematic warning signals to avian predators based on the visual contrast value between the beetle and 1) various forest substrates on which beetles are found (Endler 1988) and 2) wasps. If the visual contrast surpasses a threshold of detectability between forest substrates and wasps, they are considered to be visually apparent (Vorobyev et al. 1998) against forest substrates and wasps.

The impact that prey appearance has on predator and prey abundance and consequently species' ecological roles has not been examined previously. Here I

contribute to this area by developing two new methods that incorporate visual contrasts of beetles under avian tetrachromatic vision to link avian and beetle trophic levels. First, I use avian visual perception of prey organisms to examine the interplay between predator and prey abundance. Considering that visual contrasts are important for many birds to detect their prey leading to predation, variations in visual contrasts of beetles with backgrounds may moderate the interplay between bird abundance and beetle abundance. For instance, if beetle prey resembles forest substrates on which they are commonly found, they would be less likely to be detected and consequently depredated by insectivore birds. If beetle prey resembles other harmful insects such as wasps, the beetle may be visually detected by the bird but because of this resemblance may not be as likely to be depredated by birds. However, if beetle prey is easily distinguished from both forest substrates and wasps, it may be both visually detected and more readily depredated by birds. I also incorporate avian visual perception of beetles into the development of a novel functional trait that represents a vision-mediated predator-prey interaction between beetles and birds. Many studies make estimates of species ecological roles strictly with broad classifications such as “predator,” “decomposer,” or “pollinator,” but these classifications do not encompass the entire spectrum of ecological roles that an organism has in a community. The risk of vision-mediated predation by birds is important because birds are important predators of beetles, and a beetle’s appearance may mediate these trophic interactions.

1.7 Ecological significance of the Cerambycidae

The longhorned beetles (Family: Cerambycidae) are a charismatic beetle group often prized by insect collectors due to their colorful appearance and distinct anatomical features. As the name "longhorned" implies, these beetles typically have long antennae that are folded backwards along the body, and in some species the antennae extend much further than the entire length of the body. The lengthy antennae house highly developed sense organs used by the beetle to locate hosts and conspecifics through olfactory cues (Linsley 1961). This group, composed almost entirely of plant feeders, is one of the more diverse among the beetles with over 20,000 species described worldwide (Arnett et al. 2002) and is also an economically important group to humans across the globe. While most cerambycids in North American temperate regions are beneficial, some are pests that cause damage to trees (Shibata 1987), cut logs (Safranyik & Raske 1970), orchards (Tezcan & Rejzek 2002), nut trees (Rad 2006) and wood furnishings (Matei & Teodorescu 2011).

Longhorned beetles have diverse feeding preferences in temperate hardwood forests both in larval and adult form (Appendix A). They feed on a variety of host plants including hardwood, conifer, shrub, vine, and herbaceous species (Hanks 1999). Some species are specialists feeding on plants within a single genus, whereas others are diverse generalists that feed on as many as thirty different plant families. Host condition is also variable and larvae may feed on living, weakened, moribund, recently dead, or decaying wood (reviewed by Hanks 1999). The number of host families is dependent on host plant condition. For instance, those feeding on decaying wood are likely to be more polyphagous than those feeding on living tissue due to chemical defenses in living plants

(Linsley 1959). Females oviposit their eggs in crevices of bark, in or around plant wounds, in sites where bark has been removed, or in decomposing wood (Linsley 1961). Where on the plant females oviposit is specific to beetle species and can include tree bases and leaf nodes (Linsley 1961). After hatching larvae bore into the various layers of wood of their host plant and feeding may take place in the trunk, branches, twigs, or roots of trees (Linsley 1959). Their feeding eventually forms galleries in the wood, and after reaching a particular stage of development, larvae pupate (Linsley 1961). Pupation can occur in the bark to facilitate emergence of adults, or larvae may form pupal cells deeper in wood and plug openings with frass which acts as a barrier to protect the pupae (Linsley 1961). Once emerged as an adult, the beetle leaves the host tree to mate and find new host plants on which to oviposit (Linsly 1961). Most of a longhorned beetle's life is spent in the larval stage (Linsley 1959, Hanks 1999). Some species do not feed as adults because the time spent as an adult may be short, just a few weeks (Safranyik & Moeck 1995) or less (Hanks 1999). However, among the species that do feed as adults, species may feed on twigs, foliage, or pollen and nectar from flowers (Hanks 1999). Considering the wide breath of feeding activities, it can be expected that these beetles have diverse ecological roles in hardwood forests. For instance, larval feeding of deadwood accelerates decomposition and the release of nutrients (Gutowski 1987, Edmonds & Eglitis 1989). These contributions to deadwood decomposition reduce the severity of forest fires by reducing forest fuel loads (Gutowski 1987). Galleries created by larvae create habitat for other invertebtates within deadwood (Holland 2009). Forest health may be promoted by feeding on living trees. For instance, feeding on stressed trees may kill the trees, and their nutrients are cycled to the soil which are then utilized by healthy trees

(Berryman 1986). Also, adult beetles that feed on nectar and pollen are pollinators of flowering plants (Linsley 1961, Kevan & Baker 1983).

1.8 Ecological significance of beetles that depredate wood-borers

While not as widely studied as the longhorned beetles, several families of beetles are economically important due to their role as predators of woodborers (Böving & Champlain 1920). The checkered beetles (Coleoptera: Cleridae) consist of a charismatic group named for the colorful patterns on the elytra. These beetles hunt all stages of woodboring insects in living, stressed, moribund, and dead hardwoods and conifers (Appendix B). As adults they can be found as either sit-and-wait predators or as active predators on tree trunks and branches hunting incoming adult wood-borers searching for oviposition sites. Adults of some species are known to enter wood-borer galleries to feed on eggs, larvae, and pupae. Other species may also be found on flowers supplementing their diets with flower pollen. Adults aggregate on infested trees to mate, and females enter wood-borer galleries to oviposit eggs near wood-borer broods which later serve as food for the larvae. Larvae are also reported to feed on eggs and pupae of wood-borers.

In many cases, body form follows function in several other important predator beetle groups. Many species have a dorsoventrally flattened body form, an adaptation important for a life in crevices of deadwood. Two groups that have a flattened body include the flattened bark beetles (Coleoptera: Cucujidae) and the parasitic flat bark beetles (Coleoptera: Passandridae). Certain members of the clown beetles (Coleoptera: Histeridae) also have this body form and inhabit crevices of dead or decaying wood (Downie & Arnett 1996). Other species within this family have more of a cylindrical

shape to facilitate hunting in galleries (Downie & Arnett 1996). Little is known about the ecological habits of these beetles, but the flattened bark beetles and the clown beetles are recorded to feed on eggs and larvae of woodboring insects in dead and decaying hardwood. Interestingly, the parasitic flat bark beetle was observed to be an ectoparasite of longhorned beetle pupae. Even though all of these groups are predators of wood-boring beetles, the diverse hunting habits and habitat types contribute to them having different ecological roles in hardwood forests.

1.9 Effects of habitat loss and fragmentation on species

Habitat fragmentation and loss are primary factors contributing to loss of biodiversity (Brook et al. 2003, Pereira et al. 2010, Rands et al. 2010). Habitat loss can be characterized by a reduction in habitat area, whereas fragmentation can be described as the interspersion of habitat patches resulting in a mosaic of habitat patches surrounded by various matrix patches. The increased habitat isolation and increased ratio of edge to habitat area with fragmentation increase the probability of individuals leaving suitable habitat (Fahrig 2002). Furthermore, populations inhabiting smaller habitats tend to also be smaller thus more susceptible to extinction (MacArthur & Wilson 1967). These changes in landscape pattern can be detrimental to ecosystems, causing them to pass a threshold point and to shift to an alternative state (Beisner et al. 2003) where there is a sudden change in quality of some aspect of that ecosystem (Groffman et al. 2006) or a species' ability to maintain populations (Fahrig 2001).

Changes in landscape pattern, whether they reflect habitat loss or habitat fragmentation, affect populations differently. Decreased patch area and increased patch

isolation may reduce species persistence in the landscape (Fahrig 2003). Furthermore, edge effects may negatively impact populations 1) by increasing the time species spend in non-patch habitat (Fahrig 2002), 2) by causing negative species interactions (Chalfoun et al. 2002), or 3) because species have varying sensitivities to edge (Costa et al. 2013). For instance, landscapes with greater fragmentation have increased edge which increases the probability that individuals will leave suitable habitat (Fahrig 2003). Negative species interactions, such as increased predation on forest birds, may take place at forest edges (Chalfoun et al. 2002). Also, beetles can demonstrate edge behavior where some are confined to pine forests (the habitat patch) whereas others are found more in open areas neighboring pine forest (matrix patch) (Costa et al. 2013). In taking into account the different ways that individuals respond to habitat loss and fragmentation, it is important to consider species responses to changes in both.

The topics elaborated here are important in the following chapters. Functional diversity of longhorned beetles and their beetle predators are examined along a forest fragmentation gradient, assessed both by amount of habitat and edge. I was interested in capturing as much as possible about the beetles' functional roles, so I developed two new functional traits, landscape scale response and avian visual perception (Chapter 3). In Chapter 4 I tested the occurrence of three different proposed stability mechanisms that involve asynchronous response of species with similar functional roles. I incorporated landscape scale response into new methodology to detect the ecological stability mechanism, cross-scale resilience. Avian visual perception of beetle prey was also used to link abundances within the avian and beetle communities (Chapter 5).

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CHAPTER 2. MECHANISMS OF BIRD VISION AND CURRENT METHODS FOR STUDYING VISION-MEDIATED AVIAN BEHAVIOR WITH EMPHASIS ON INSECT PREY

2.1 Introduction

Among the vertebrates, birds are known to have extraordinary vision capabilities. The demands for having exceptional vision are high in most birds; not only must their vision serve them in flight which requires high color and movement discrimination (Hart 2001), but many behaviors often found in some species including mate choice (Bennett et al. 1996), food selection (Cazetta et al. 2009), and predator evasion (Blackwell et al. 2009), are also mediated by vision. Anatomical and physiological features of diurnal birds' eyes have been studied extensively, and we have learned that these structures have specific adaptations that make them superior instruments when matched against those of a human. Compared to the human eye, the diurnal bird eye differs in anatomical arrangement (summarized in Table 2.1), and specifically related to the retina, has 1) more cone types leading to a wider spectral range of photoreceptor sensitivity and 2) pigmented oil droplets within cone photoreceptors whose function is to filter light entering the cones, thus intensifying color perception.

This review is aimed to provide supplementary material for a study in which I use avian vision of beetle prey to directly examine changes in species abundance across trophic levels. This work, described in Chapter 5, is a novel approach to examine

Table 2.1: Summary of the most significant anatomical differences between human and diurnal, insectivore bird eyes

			
Anatomical feature	**Eye size**	eye size:body size is small	eye size:body size is large (Fernández-Juricic et al. 2004)
	Gaze	forward-facing (Denion et al. 2015)	side-facing
	Mobility	highly mobile due to extraocular musculature (Purves et al. 2001)	limited eye mobility due to tight orbit (Walls 1942)
	Foveae	just one, the *fovea centralis* (Provis et al. 2013)	two: a central fovea (Fernández-Juricic et al. 2004) and, according to Galifret, a temporal fovea (as cited in Fernández-Juricic et al. 2004)
	Iris control	involuntary; controlled by smooth muscle sphincter (Provis et al. 2013)	voluntary' controlled by striated muscle (Pumphrey 1947)
	Pecten	no	yes, but function unknown

changes in community structure with visual contrasts. I first elaborate on the above-mentioned differences between human and diurnal, insectivore bird eyes which distinguish vision between these groups. Given that birds have superior vision capability, understanding their visual system is facilitated by having a familiar point of reference: our visual system. Importantly, the comparison of these differences gives further evidence that we must take into account how prey would appear to a bird if we want an ecologically relevant perspective of how a bird views insect prey. I discuss methodology to discriminate avian spectral tuning based on molecular data and describe methods that have been developed to refocus the anthropocentric visual perspective of objects into that of a "bird's eye view." Such methodology is now implemented to investigate bird behavior. I then briefly review studies that have demonstrated that UV vision mediates many bird behaviors.

2.2 Differences between human and avian vision

2.2.1 Anatomical differences between human and avian eyes

Human and avian eyes have some major anatomical differences. Here, I focus on the primary disparity between human and diurnal, insectivorous bird eyes. The human eye is forward-facing and within an orbit with a high width/height ratio (Denion et al. 2015). It is also very mobile due to being controlled by three pairs of extraocular muscles which rotate the eye along the horizontal, vertical, and torsional axes (Purves et al. 2001). This movement by extraocular musculature is very important because of the physical limitations presented by the properties of the retina. The retina contains a single area with high visual acuity with respect to color and spatial detail (Provis et al. 2013).

This area, called the fovea (meaning "pit"), is positioned so that the center of the visual field is located at the 'nasotemporal division' of the retina, thus is called the *fovea centralis* (Provis et al. 2013) (Figure 2.1). Furthermore, the human retina is shaped such that objects farther from this optic axis are not in focus (Pumphrey 1947). Therefore, greater control of eye movement helps to accommodate by extending the human visual field through eye motion. Also, the human iris is controlled by smooth muscle arranged as a sphincter around the periphery of the pupil (Yoshitomi et al. 1988, Junqueira & Carneiro 2003).

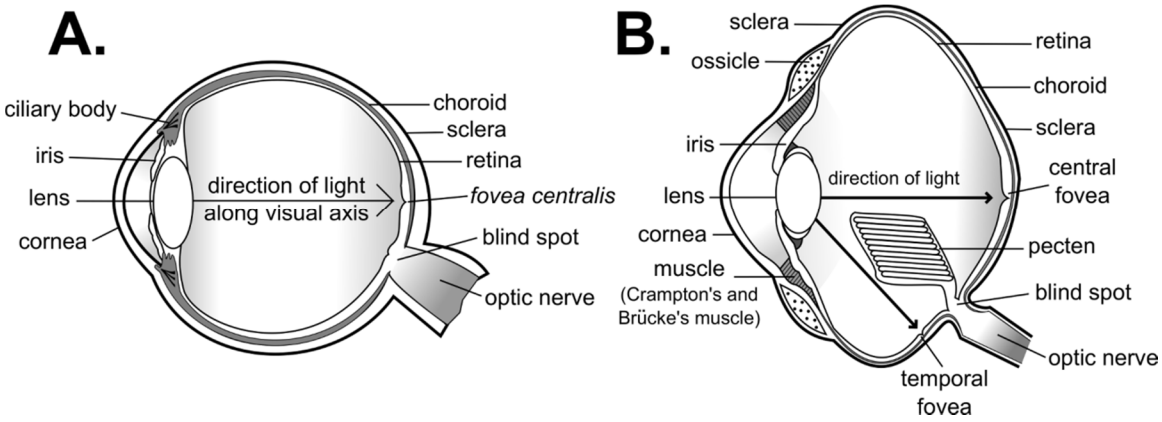

Figure 2.1. Diagrams of human and avian eyes to show the anatomical differences between them. A. Human eye, adapted from Junqueira & Carneiro (2003). B. Avian eye, adapted from Rowe (2000).

The avian eye, in contrast, is quite large in proportion to a bird's body size (Fernández-Juricic et al. 2004), an adaptation that Galifret contributes to the visual acuity of birds (as cited in Fernández-Juricic et al. 2004). However, eye movement is a tradeoff for visual acuity; the avian eye lacks the mobility of the human eye. The eyes are large, filling much of the cranium, and are tightly surrounded by the orbit (Walls 1942). This

prevents sufficient space in the cranium to house extensive extraocular musculature to rotate the eyes (Walls 1942). There are several adaptations found in the avian retina, however, that compensate for this loss in eye mobility. First, the retina of many species contains multiple foveae: a central fovea that defines a lateral visual field giving rise to monocular vision (Fernández-Juricic et al. 2004) and, according to Galifret, a temporal fovea (as cited in Fernández-Juricic et al. 2004) which extends the visual acuity forward, facilitating the identification of food items and pecking control (Fernández-Juricic et al. 2004) (Figure 2.1). Second, the shape of the retina in the avian eye, being almost entirely in the image plane, allows for objects distal to the optic axis to still be focused on the photoreceptors (Pumphrey 1947).

A further difference between the human and avian eye is that the avian iris is controlled by two sets of striated, voluntary muscles, the Crampton's muscle and the Brücke's muscle (Pumphrey 1947) (Figure 2.1). Contractions of the Crampton's muscle cause the center of the cornea to bulge by pulling inward on its margin, while the Brucke's muscle increases the curvature of the lens by squeezing it (Pumphrey 1947). Also, avian eyes contain ossicles, or boney, "horseshoe-shaped" structures, within the orbit composed of separate pieces that vary in number among species (Walls 1942) (Figure 2.1).

The most unique anatomical feature in the avian eye is a structure devoid of nervous tissue (Brach 1977) called the pecten (Figure 2.1) that covers the "blind spot", an area where the optic nerve enters to conduct sensory information (Ferree & Rand 1912), thus lacks photoreceptors (Junqueira & Carneiro 2003). The pecten is a pleated structure whose shape varies among bird taxa, but the most common type of pecten is the "pleated

fan" (Brach 1977). Wagner noted that a large pecten size is correlated with diurnality (as cited in Walls 1942). Regardless of pecten shape and size, its pleated form is assumed to increase its surface area (Brach 1977). The purpose of the pecten is unknown (Brach 1977), but its increased surface area may provide evidence for its function. For instance, unlike the human eye chamber, the avian eye chamber is devoid of blood vessels which may aid in avian visual acuity (Walls 1942). However, oxygen must be supplied to the inner retinal cell layers. Considering that the pecten contains an abundance of blood vessels, Walls (1942) proposed that nutrients must diffuse from the pecten into the vitreous humour and then to the retina to deliver nourishment to these retinal layers. Others including Menner (as cited in Brach 1977) and Crozier and Wolf (1943, 1944) proposed that the pecten may aid in the detection of movement by increasing the flicker response contour of the eye. The development of this structure is greatest in birds that rely on motion detection while foraging, which may provide further clues to the pecten's function. For instance, pectens are most developed in hawks, followed by diurnal insectivores, then granivores, and lastly nocturnal birds (Pumphrey 1947). Despite these interesting findings, the pecten casts a minimal shadow on the retina that falls almost entirely on the "blind spot" making it unlikely that birds can see the pecten (Brach 1977). Another interesting hypothesis on the pecten's function is that it mayregulate pH balance in the eye chamber in response to pH imbalance resulting from retinal metabolism in an anaerobic environment (elaborated in Brach 1977).

2.2.2 The retina (Figure 2.2)

The retina of both humans and birds consists of a nexus of four cell layers; the innermost layer relative to light hitting the retina is composed of pigmented epithelium tissue (Pumphery 1947, Junqueira & Carneiro 2003). Beyond this cellular layer, the pigmentation within a separate layer called the choroid functions to further prevent reflection of light that was not absorbed by the retina helping to prevent blurred imaging that would result from light scattering (Walls 1942, Junqueira & Carneiro 2003). The cellular layer of the retina above the choroid consists of the photoreceptors which contain the pathways that are first involved in translating light into a neurological signal. The bipolar cells connect the photoreceptors to the fourth cell layer, the ganglion cells, which send the translated neurological signal of light from the stimulation of photoreceptors to the optic nerve (Junqueira & Carneiro 2003).

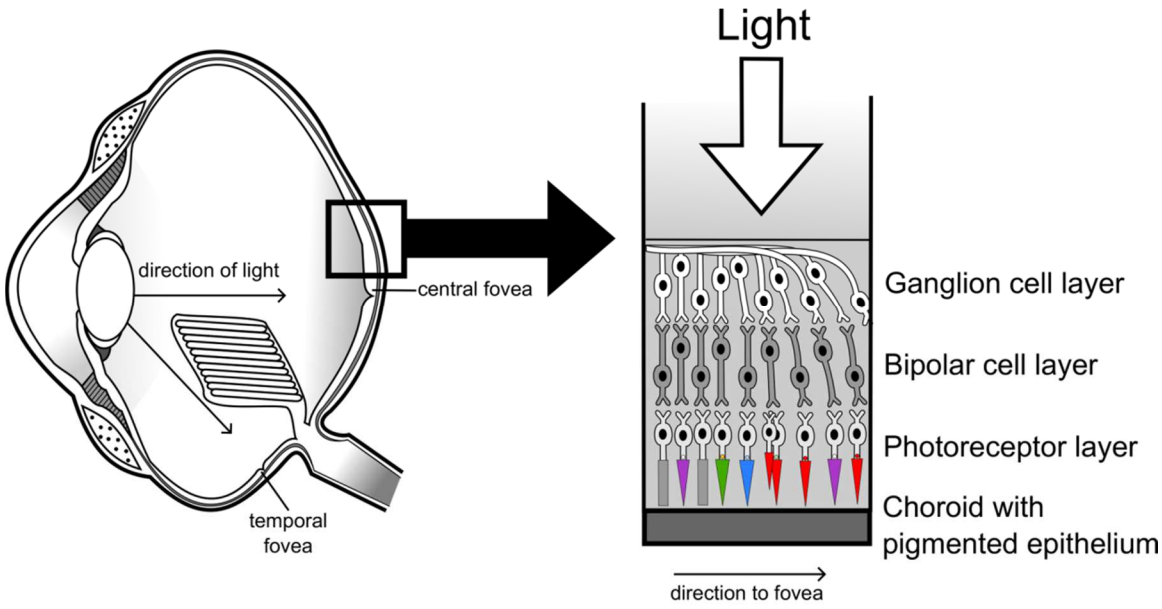

Figure 2.2. The avian retina in an area approaching the fovea to illustrate its cell layers including the photoreceptor layer. The choroid contains pigmented epithelium to prevent the reflection of light not initially absorbed by the photoreceptors. Adapted from a figure illustrating the human retina in (Junqueira & Carneiro 2003).

Retinas of humans and diurnal birds contain specialized regions where cone photoreceptor cell densities are high compared to other regions (Provis et al. 1998) and rods are absent (Walls 1937). Here, the cones have a slender, elongate shape to facilitate aggregation (Walls 1937). These cone-packed areas are referred to as the fovea, within which ganglion and bipolar cell layers accumulate producing a depressed, conical-shaped pit (Walls 1937, Junqueira & Carneiro 2003). Visual acuity is greater in this region due to the packing of cones rather than rods due to the cone's ability to produce sharper vision and due to the sloped walls of the fovea (Walls 1937, Harkness & Bennet-Clark 1978, Junqueira & Carneiro 2003). Retinas of diurnal birds have steeper-sided foveae than the retina of humans (Walls 1937), suggesting these birds have superior visual acuity (Harkness & Bennet-Clark 1978).

2.2.2.1 Spectral range and photoreceptor types

Photoreceptors are elongated cells with two portions: the outer and inner segments (Junqueira & Carneiro 2003). The inner segments house the cellular machinery necessary for energy production and other cellular processes (Junqueira & Carneiro 2003) while the outer segments each contain different photopigments which make them respond to distinct wavelengths of light (Cuthill 2006). Rods are photoreceptors for scotopic (or dark-adapted) vision (Wyszecki & Stiles 1982, pp. 252) and are involved when light conditions are low and greater sensitivity is needed by the viewer (Provis et al. 1998). The outer segments of rods consist of "flattened disks" that contain the photopigments, which when exposed to a photon of light, produces a visual stimulus (Junqueira & Carneiro 2003). Cones, however, are photoreceptors adapted specifically

for photopic vision (vision used under well-lit conditions) and are used in interpreting color (Hart 2001). They are similar to rods in that their outer segments are composed of stacked disks, but their conical shape is due to invaginations of these stacked disks (Junqueira & Carneiro 2003). The outer segments contain also contain photopigments which vary in their spectral sensitivity (Junqueira & Carneiro 2003). Under mesopic (intermediate) illumination, both rods and cones are used for vision (Wyszecki & Stiles 1982, pp. 252).

Humans and birds differ with respect to visual photopigments found in their photoreceptors. Normal human individuals generally have four different photoreceptors, rods and three cones, each with a distinct spectral sensitivity (Junqueira & Carneiro 2003). Human rods have photopigment sensitivity at ~505 nm (Brown & Wald 1964) while cones have photopigment sensitivity at red (long wave sensitive, LWS, 560 nm), green (medium wave sensitive, MWS, 530 nm) (Schnapf et al. 1987) and blue (short wave sensitive, SWS1, ~ 420 nm) (Dartnall et al. 1983) wavelengths. The blue cone in the human eye contains a moderately UV-sensitive pigment, but the ocular media of the eye is not transparent to UV light (Bennett & Cuthill 1994). Therefore, a human's visual spectrum is 400 – 700 nm (Figure 2.3). The avian retina, in contrast, contains a mosaic of six types of photoreceptors: rods, four types of single cones and two associated double cones which function together as one unit (Kram et al. 2010) (Figure 2.4). These photoreceptors are highly conserved across bird species (Hunt et al. 2009). Microspectrophotometric spectra reveal that avian photoreceptors have differing spectral sensitivities. Rods have spectral sensitivity between 500 – 509 nm (Hart 2001). Double cones consist of one larger and one smaller cell in close physical contact (Cuthill 2006)

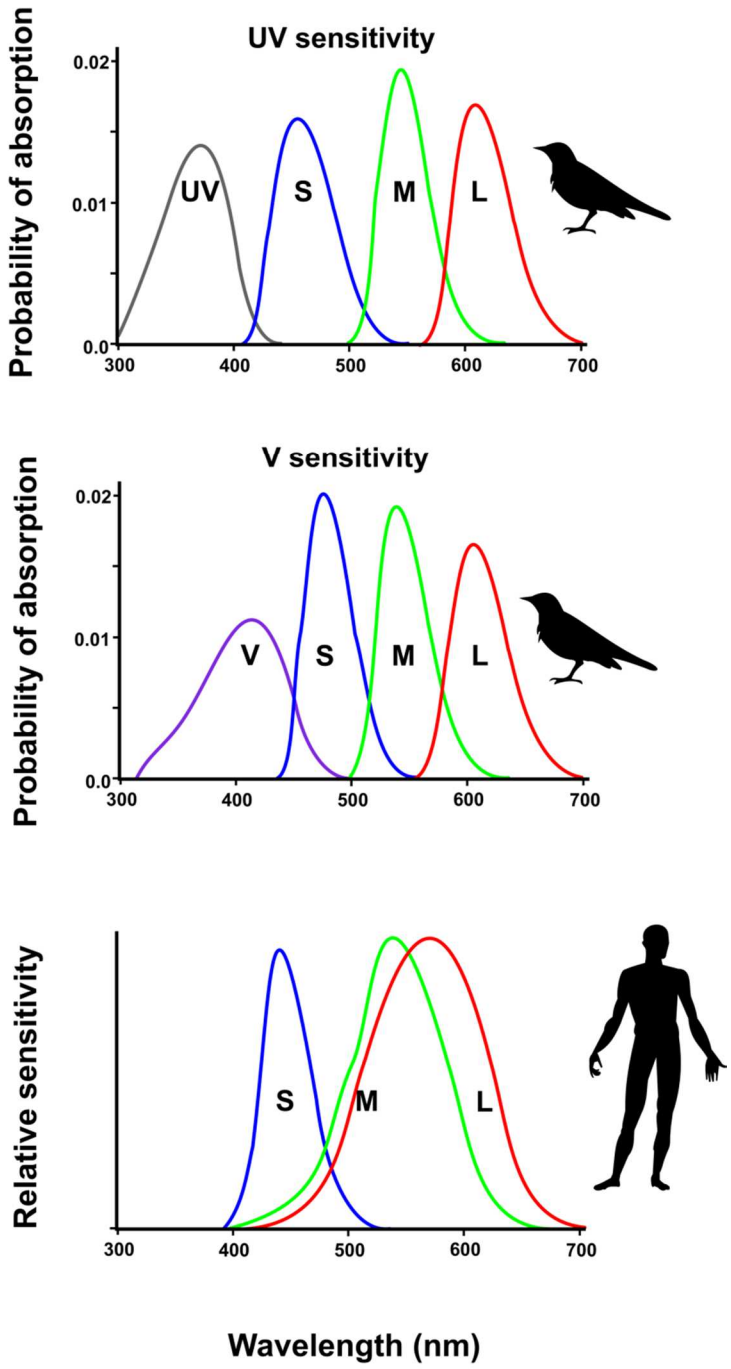

Figure 2.3. Spectral sensitivities of the avian retina (given in probability of absorption) and the human retina (given in relative absorption). "UV" and "V" indicate the spectral sensitivities of the SWS1 (short wave sensitive) cones. UV = UV-sensitive; V = violet-sensitive; S = short wave sensitive; M = medium wave sensitive; L = long wave sensitive. The avian retina spectral sensitivities were adapted from Endler & Mielke (2005). The human retinal spectral sensitivities were adapted from Goldsmith (1990).

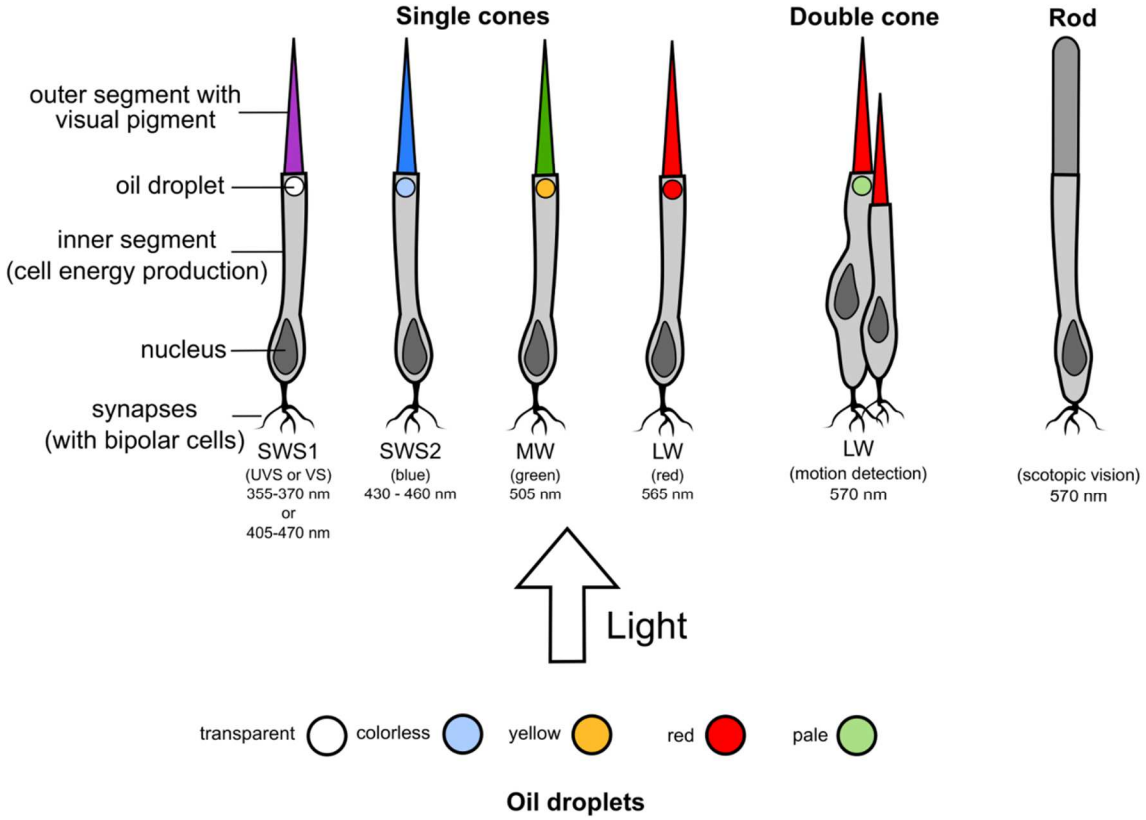

Figure 2.4. Avian rods and cones including four single cones (one being either UV- or violet-sensitive), double cones, and rods. The oil droplets of cones are also shown to illustrate their position in the distal portion of the cone's inner segment and their pigmentation type. Adapted from Toomey et al. (2015).

and are the most abundant of the retina's mosaic of photoreceptors (Bowmaker et al. 1997) where they compose approximately 50 percent of all cones (Bowmaker 2008). The double cones have a spectral sensitivity at 570 mm (Cuthill 2006) and Campenhausen and Kirschfeld hypothesized that they are utilized in motion detection (as cited in Hart 2001). There are four single cone types used in photopic vision (vision used under well-lit conditions) in the avian retina (Figure 2.4). Among them, three are SWS2 (~430 – 460

nm), MWS (~505 nm), and LWS (565 nm) sensitive, the latter having the same spectral sensitivity as a double cone (Cuthill 2006). The fourth single cone type (SWS1) can peak in sensitivity within the ultraviolet (UV) (355 – 370 nm) or violet (V) range (405 – 420 nm) depending on the bird species (Cuthill 2006), indicating that birds have the physical capability of distinguishing colors beyond the limits of the human visual spectrum (Figure 2.3).

2.2.2.2 Oil droplets function as an ocular filter

One major difference that distinguishes human and avian cones is that each avian cone, having a specific spectral sensitivity, is associated with a specific type of oil droplet located in the distal portion of the cone's inner segment (Cuthill 2006) (Figure 2.4). Oil droplets are composed of neutral lipids and various types of carotenoid pigments (Hunt et al. 2009). The carotenoid pigments within the oil droplet, depending on the spectral transmittance of the droplet along with the spectral absorbance of the cone's visual pigment, act as spectral filters (Cuthill et al. 2000) and modify the spectral sensitivity of photoreceptors (Hunt et al. 2009). Pigments in the droplets cut off shorter wavelengths (Hunt et al. 2009), narrowing the cone sensitivity, reducing the overall quantum catch of the photoreceptor causing improved color discrimination (Vorobyev 2003).

Oil droplets contain several types of carotenoid compounds, but this mixture is dominated by a single class of carotenoid (Toomey et al. 2015). Transparent (commonly abbreviated as "T") oil droplets lack carotenoids and are contained within UV and V cone cells (Goldsmith et al. 1984) thus have no significant absorbance along the visual spectrum above 320 nm (Goldsmith et al. 1984). Cones with blue sensitivity and double cones have colorless (C) oil droplets which appear opaque at 405 nm (Goldsmith et al.

1984). These droplets contain an apocarotenoid, galloxanthin, a compound that absorbs in the UV and blue wavelengths and has a cut-off at ~450 nm (Bowmaker et al. 1997, Toomey et al. 2015). Cones with green sensitivity have yellow (Y) oil droplets with a hydroxycarotenoid, zeaxanthin (Toomey et al. 2015), which also absorbs intermediate wavelengths with a cut-off at ~510 nm (Bowmaker et al. 1997). Cones with red sensitivity have red (R) oil droplets with a ketocarotenoid, astaxanthin (Toomey et al. 2015), which absorbs green and orange wavelengths, having a filtering cut-off at 570 nm (Bowmaker et al. 1997). The major arm of double cones contains pale (P) oil droplets that contain an apocaroteonid, galloxanthin, which absorbs in blue wavelengths (Toomey et al. 2015), having a filtering cut-off at ~570 nm (Bowmaker et al. 1997**)**. The accessory cone of the double cone cell, however, may lack an oil droplet (Bowmaker 1980).

2.3 Predictions of spectral tuning of the SWS1 cone type

The accumulation of knowledge on vertebrate vision shows a stark contrast between human and diurnal avian eye anatomy and physiology giving strong evidence that the eyes of diurnal birds are capable of extraordinary vision. However, despite what we have learned about bird vision, studies on avian spectral tuning (whether having UV- or V-sensitive pigments) have been restricted to a few species. This is due to the preparation of retinas for microspectrophotometry which involves maintaining live subjects in darkness for several hours, sacrificing them, and dissecting their eyes to obtain retina specimens (methods described in Hart et al. 1998, difficulties of sample preparation given in Carlson 1972). Despite this limitation, studies have utilized opsin amino acid structure to deduce the spectral tuning of birds.

Light is translated into a neurological signal beginning within the protein complex, rhodopsin, located in the outer segment of the photoreceptor, which consists of opsin and the chromophore. Opsin molecules in the rhodopsin complex differ in their amino acid sequence which leads to changes in the opsin protein's structure (Applebury & Hargrave 1986). Overall, these changes in opsin structure influence the protein's spectral obsorption (Applebury & Hargrave 1986) thus can lead to the identification of spectral tuning sites (Yokoyama 2000). The difference in violet-sensitive (VS) vs. UV-sensitive (UVS) spectral tuning is attributed to a single amino acid change in the SWS1 polypeptide (Wilkie et al. 2000, Yokoyama et al. 2000). Using information on the SWS1 opsin amino acid structure, Ödeen & Håstad (2003) developed molecular methods to estimate the spectral tuning in avian species by sequencing the gene coding for SWS1 opsin. DNA samples were obtained from 46 bird species dispersed across 35 families, and results indicated that within the selected taxa, UVS vision evolved from VS vision independently four times (Ödeen & Håstad 2003). Current data suggest that VS vision is more common, but vision type has a complex distribution in the phylogeny of birds (Ödeen & Håstad 2003). Ödeen et al. (2009) further confirmed that these sequencing methods are an accurate approach to determining the spectral tuning of a species by comparing their results to published microspectrophotometric data. Using the same methods of sequencing the SWS1 opsin gene, Ödeen et al. (2011) investigated the distribution of UVS and VS vision strictly in the Passeriformes. Their study indicated that the ancestor of this group had UVS vision and that within this group vision type changed between VS and UVS a minimum of eight times (Ödeen et al. 2011).

2.4 Modeling avian tetrachromatic color space

The disparities between human and avian vision have inspired the development of methodology to estimate a bird's visual perspective of its surroundings. This methodology, the foundation of which revolves around color perception, has been used to study the ecological importance of UV vision in birds. Color perception is based on the stimulation of one photoreceptor relative to the others in the retina (Cuthill 2006). In "opponent processing", the cell layers in the retina (gangion, bipolar, and amacrine cells) "compare" the relative stimulation of photoreceptors amongst the different photoreceptor types and stimulate inhibitory and excitatory responses (Cuthill 2006). Color vision, therefore, results in part from this coded information dependent on the interactions amongst these nerve cells (Cuthill 2006). Therefore, birds with four different cone photopigment sensitivities would be considered tetrachromats becauseall the perceived colors can be interpreted from the combination of the four monochromatic colors, UV or violet, blue, green and red (Cuthill 2006). Thus, dimensionality of avian color vision can be constructed by representing all the colors visible by an organism as axes of a multidimensional color space whose volume can be represented by:

$$Q_{UV/V} + Q_{blue} + Q_{green} + Q_{red} = 1 \quad (1)$$

where $Q_{UV/V}$, Q_{blue}, Q_{green}, and Q_{red} are the cone captures for the UV or violet cone, blue cone, green cone, and red cone, respectively. This color space is represented by a tetrahedron whose axes are the proportion of photon captures of each of the four cone types (Figure 2.5).

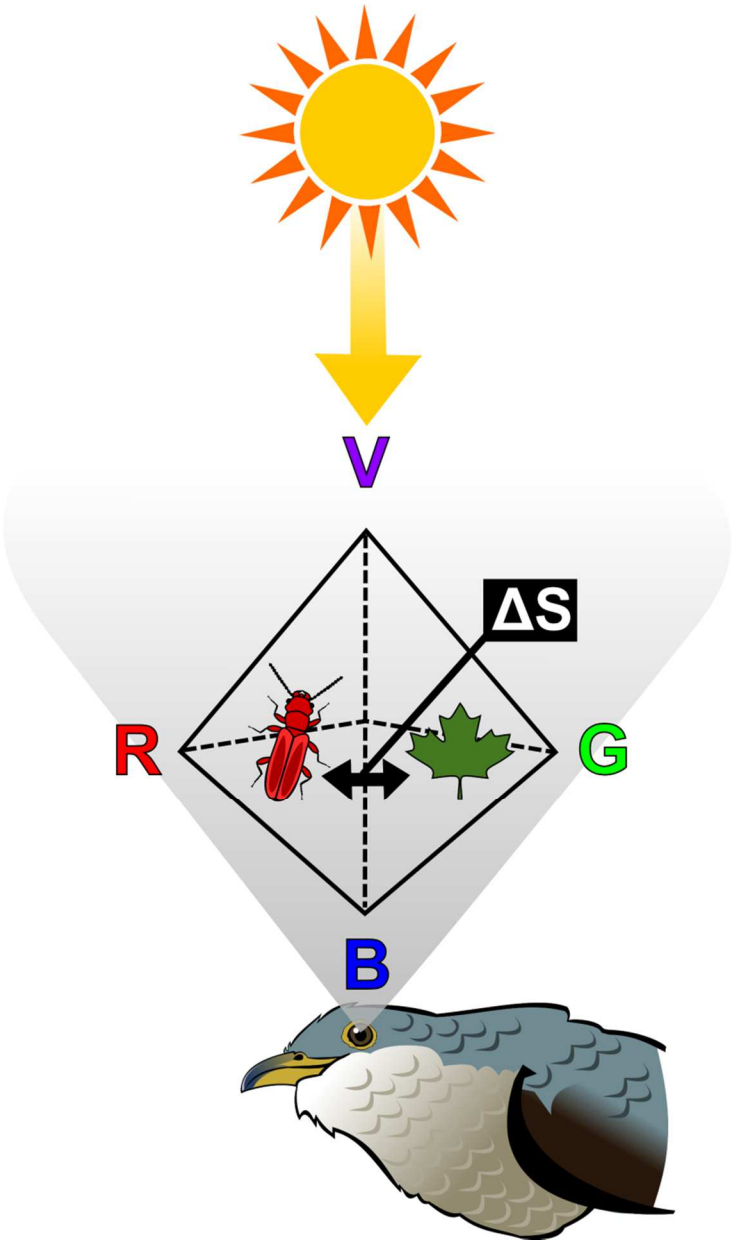

Figure 2.5. Hypothetical depiction of the visual contrast between *Cucujus clavipes*, a predator beetle, and a maple leaf, *Acer saccharum*, under full sunlight within avian tetrahedral color space of the yellow-billed cuckoo, *Coccyzus americanus*. V = violet-sensitive photoreceptor; R = red-sensitive photoreceptor; G = green-sensitive photoreceptor; B = blue-sensitive photoreceptor; ΔS = chromatic contrast.

Many studies have used spectroradiometry and physiological models of color vision to investigate how birds visually perceive their environment. Here I describe the visual model proposed by Vorobyev et al. (1998) which integrates 1) physiological characteristics of the avian retina including visual pigments, oil droplet spectral absorption, and the density and distribution of receptors across the retina, and 2) data that describe how light is transmitted to the viewer from two desired objects of comparison. The latter include the reflectance of these objects and the irradiance measurements of the ambient light conditions under which two objects are viewed. The reflectance is a physical property of an object's surface (Andersson & Prager 2006), whereas irradiance is a property of ambient light (Endler & Mielke 2005). The outcome of this model is the chromatic contrast between two objects.

The physiological aspects of the avian retina are obtained, and "opsin spectral sensitivities are described by fitting a standard nomogram (Maximov 1988) to the peak sensitivities measured by microspectrophotometry. . . Oil droplet functions are modeled as hyperbolic tangents fitted to the midpoint and slope of the measured absorption of oil droplets (Maier and Bowmaker 1993; Bowmaker et al. 1997)" (Vorobyev et al. 1998, p. 625). The model then considers the ocular media's spectral absorption (Vorobeyev et al. 1998). These components are incorporated in the model of Vorobyev et al. (1998) as follows.

The first equation in the model calculates quantum catch, Q_i, or the proportion of photons captured by the photopigments in each photoreceptor of the avian eye, i (i = 1, 2, 3, …, n), given by Eq. 2:

$$Q_i = \int_{\lambda=300}^{\lambda=700} R_i(\lambda)\, S(\lambda)\, I(\lambda)\, \mathrm{d}\lambda \ , \quad (2)$$

where $R_i(\lambda)$ is the spectral sensitivity of photoreceptor i, $S(\lambda)$ is the reflectance spectrum, $I(\lambda)$ is the spectrum of light entering the eye, and λ is wavelength, in nanometers. Integration is over the entire visible spectrum of the viewer (~300 nm – 700 nm among bird species) at 1-nm intervals.

Once quantum catch is calculated, the model considers chromatic adaptation of photoreceptors. This phenomenon occurs when the visual system adjusts to differences in illumination, the outcome being an object that is perceived as the same color by the viewer regardless of differences in how light illuminates the object (Wyszecki & Stiles 1982, p. 429). A simple example of chromatic adaptation in humans would be grass appearing green whether it is viewed under natural sunlight or the light given off from a Tungsten bulb. Next, the model incorporates the von Kries transformation which accounts for the adaptation of photoreceptors by normalizing Q_i to the background, given by:

$$q_i = k_i Q_i \ , \quad (3)$$

where k_i is a coefficient whose selection is based on having constancy in the quantum catches for adapting background. Mathematically, the constant represents a diagonal matrix that is used to scale photoreceptor absorptions (Wyszecki & Stiles 1982, pp. 431). Specifically, the coefficient k_i is given by:

$$k_i = 1 \,/\, \int_{300\,\mathrm{nm}}^{700\,\mathrm{nm}} R_i\ (\lambda) S^b(\lambda) I(\lambda) \mathrm{d}\lambda\ \ , \tag{4}$$

where here S^b equals the background's reflectance spectrum.

After accounting for chromatic constancy, the model then applies Weber's law to account for receptor noise. Weber's law quantifies the relationship between the intensity of a given stimulus and how much that intensity needs to change in order for that change to be noticed (Wyszecki & Stiles 1982, p. 490). When applied in the model of Vorobyev et al. (1998), Weber's law is expressed as:

$$\Delta f_i = \ \Delta q_i \,/\, q_i\ \ , \tag{5}$$

where f_i is the signal of receptor mechanism i, Δf_i is the difference between the signals in receptor mechanisms between stimuli, and Δq_i is the difference in the quantum catch between stimuli. If Weber's law is observed, when $\Delta q_i/q_i$ is plotted as a response variable and q_i is plotted as an explanatory variable a horizontal line with a y-axis intercept at Δf_i will be produced. At high intensities, this intercept of Δf_i is a constant known as the Weber Fraction (Wyszecki & Stiles 1982, p. 490). When Eq. 4 is integrated, Fechner law is obtained (Eq. 5). In the model of Vorobyev et al. (1998), the signal of photoreceptors, f_i, to a given normalized quantum catch, q_i, is given by:

$$f_i = \log(q_i) \tag{6}$$

where the signal of receptors is proportional to the logarithm of the quantum catch (Vorobyev et al. 1998). However, at low intensities the Weber fraction equals the inverse proportion of receptor noise which is determined by quantum fluctuations. Here, receptor noise is given by the square root of the quantum flux (Wyszecki & Stiles 1982, p. 673, cited in Vorobyev et al. 1998), given by:

$$\omega_i = 1 / \sqrt{q_i n_i} \ , \tag{7}$$

where q_i is the normalized quantum catch of the receptor cell i, and n_i is the number of receptor cells of type i within the retina. However, if the Weber fraction is independent of intensity, it is described as:

$$w_i = v_i \sqrt{n_i} \ , \tag{8}$$

where v_i is the noise-to-signal ratio of a single cone.

Once receptor noise is established, the next part of the model includes calculates the visual distance, ΔS, between two objects in avian tetrahedral vision space (first proposed by Burkhardt (1989) and Goldsmith (1990)), based on stimulation of photoreceptors in the avian retina. ΔS represents the visual contrast between the two objects and is an indication of how apparent or cryptic the objects would be to the avian viewer under different ambient light conditions (Vorobyev et al. 1998) (depicted in Figure 2.5), given by:

$$
\begin{aligned}
(\Delta S)^2 = [&(\omega_1\omega_2)^2\,(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2\,(\Delta f_4 - \Delta f_2)^2 \\
&+ (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2\,(\Delta f_4 - \Delta f_1)^2 \\
&+ (\omega_2\omega_4)^2\,(\Delta f_3 - \Delta f_1)^2 \\
&+ (\omega_3\omega_4)^2\,(\Delta f_2 - \Delta f_1)^2 \,/\, [(\omega_1\omega_2\omega_3)^2 \\
&+ (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2] .
\end{aligned}
\tag{9}
$$

where ΔS represents the chromatic contrast between the two objects. Whether ΔS is large enough for the two objects to be discernible to the viewer is determined by a detection threshold. Overall, color can be described in three hypothetical dimensions: hue, brightness, and saturation (Collier et al. 1976). Hue is wavelength related and can be associated with the colors described on a color wheel (i.e. "blue", "yellow" or "purple"), brightness is intensity related (Schaefer et al. 2006) and refers to the value of the color on a scale of dark to light (Kelber et al. 2003), and saturation relates to a color's purity (Collier et al. 1976). Visual contrasts between objects can describe either differences in color intensity (achromatic contrasts) or differences in hue and saturation (chromatic contrasts) (Kelber et al. 2003). Since development, the model has been used to examine how birds perceive their environment with respect to perception of bird plumage patterns (Benites et al. 2010), visual discrimination of the eggs of nest parasites from the eggs of the host (Stoddard & Stevens 2011), predator-prey interactions (Maan & Cummings 2012), and fruit discrimination (Schaefer et al. 2006, Schaefer et al. 2007, Fradzly et al. 2013) with the use of chromatic contrasts.

2.5 Significance of UV vision on avian behavior

Models that depict objects in tetrachromatic color space are the most accurate methods so far developed for humans to determine how birds visually perceive their environment, making their use a forefront in bird vision ecology. UVS vision is not unique to birds (Walls 1942), but there are many proposed reasons for birds having visual sensitivity to UV wavelengths. UV-mediated behavior related to foraging and signaling has received the most attention, however. I briefly review a few examples with a heavier focus on avian–insect interactions mediated by UV signals.

Insects are a major food source for birds, and insect patterns are important signals to their avian predators. An early study that strictly focused within the confines of the human visual spectrum found that dorsal patterns of invertebrates are important in foraging decisions made by birds (Jones 1934). It was observed that when offered an assortment of insects with variable appearances, birds preferred cryptic- over aposematic-patterned prey. The avian eye is also able to distinguish reflectance in long-wavelengths, so it is to be expected that what consists as a conspicuous pattern to us (e.g., yellow, orange or red on black, particularly in contrast to green and brown forest substrates) is also highly visible to birds (Lindstedt et al. 2011).

However, it has been discovered that patterns of some insects within the Odonata, Coleoptera, Diptera, Hymenoptera, and Lepidoptera also reflect UV light (review provided by Silberglied 1979) and that the UV component of these patterns may be seen as an aposematic signal to avian predators (Cuthill et al. 2000) or may serve to deflect predator attacks. Olofsson et al. (2010) found that UV reflection in peripheral eyespots of Lepidopteran wings redirected avian predator attacks to these regions of the prey's

body that are distal from more essential parts. In other cases, UV reflectance in a prey animal's patterning may actually attract predators. Lyytinen et al. (2004) found that UV-reflecting wing patterns were more common on nocturnal vs. diurnal Lepidoptera species, which may relate to predation risk: individuals with UV patterns suffered greater mortality when exposed to diurnal predators (primarily birds), suggesting that this pattern is more apparent to these predators. Several studies, however, have investigated contribution of UV reflectance in aposematic signals to insectivorous birds. Remington (1973) compared color patterns extending to UV wavelengths of lepidopteran mimics and their models and found that their appearance was different in most cases. These differences in the UV component of aposematic patterns further demonstrate the need to examine patterns between a potentially distasteful species and the mimic within bird vision space.

Interestingly, in addition to signals to birds, UV reflectance patterns in lepidopteran species have been suggested as taxonomic features to distinguish ambiguously similar species and may also be important for mate detection by females (Silberglied & Taylor 1973). UV reflectance has been further studied in *Colias eurytheme*, a sulphur butterfly also having long-wave aposematic color patterns. The UV reflectance in this butterfly's patterns is augmented by pterin pigments (Rutowski et al. 2005), and it was originally thought that this reflectance was strictly a "private channel" for intraspecific communication among individuals within this species (Rutowski 1985, Brunton & Majerus 1995). For instance, Papke et al. (2007) found that UV reflectance in males is a strong predictor in male mating success. This phenomenon has been observed

in other species of butterfly including *Hypolimmas bolina* (Kemp 2007), *Bicyclus anynana* (Robertson & Monteiro 2005), and *Eurema hecabe* (Kemp 2008).

Fruits are another common food source for many birds, and many fruits reflect UV light. Burkhardt (1982) categorized various fruits based on their UV reflectance and found that dark-colored and shiny fruits do not reflect UV, whereas white fruits either have strong or no UV reflection. Interestingly, the wax layer of glaucous fruits extends into the UV, thus Burkhardt (1982) hypothesized that in addition to acting as a protecting layer of the fruit, the wax layer also enhances the fruit's visibility to avian foragers. Siitari et al. (1999) demonstrated that the wax layers of fruit do provide UV signaling to birds. In their study, birds preferred UV-reflecting berries over berries whose UV reflection was reduced by rubbing off their wax layer, but birds demonstrated no preference between berries when UV illumination was absent (Siitari et al. 1999).

In addition to foraging, it has been demonstrated that UV reflectance plays a significant role in signaling in intraspecific and interspecific avian interactions (Stevens & Cuthill 2007), particularly regarding mate selection (Cuthill et al. 2000). For instance, females of several species prefer males that have plumage patterns with strong UV reflectance (Bennett et al. 1996, Hunt et al. 1998, Siitari et al. 2002). UV reflectance has also been shown to influence interspecific communication in different bird species which may lead to reproductive isolation. For instance, interbreeding between *Anisognathus notabilis* and its congener *A. flavinuchus* occurs unless UV-reflecting plumage is present in *A. notabilis* (Bleiweiss 2004).

2.6 Conclusions

Studies have elucidated much information on the anatomy and physiological mechanisms of avian vision, giving evidence that birds have extraordinary color vision particularly when compared to our own visual capabilities. Various features of the bird eye contribute to their visual acuity. The avian eye contains multiple foveae which extend their field of view, and the avian retina has more cone types which enable birds to view their environment under a wider spectral range which extends into the ultraviolet. Being tetrachromats, birds are also able to distinguish more colors, and pigmented oil droplets within cone photoreceptors further enhance their visual experience by improving color discrimination. Molecular analyses have revealed that the ancestral visual system in birds was violet-sensitive (VS) and that UV-sensitive vision has evolved multiple times. Previous research has determined that the difference between having VS vs. UVS vision is the result of a single amino acid change in the SWS1 opsin polypeptide. Therefore, analyzing DNA sequences coding for this protein may be an appropriate method for determining which visual system a bird species possesses, allowing researchers to bypass complicated microspectrophotometry methods. Models of avian tetrachromatic color space have been developed to further estimate bird vision and how it mediates avian behaviors. These models, which render visual contrasts between two objects, are the best approximations of avian vision thus far and have been utilized in many studies. Birds use these UV visual capabilities in behaviors including searching and selecting food resources and potential mates. Such signals may be invisible to humans, further emphasizing the need to utilize such models of avian vision space to most accurately assess how birds visually perceive their environment.

Future directions in bird vision research may include obtaining more complete microspectrophotometric studies of avian retinas with the intention of further analyzing how the mosaic of photoreceptors in the retina differs among species. Also, even though SWS1 opsin genes have been sequenced from representative members of many bird families, work could continue in this arena to obtain estimates of the remaining families. Obtaining microspectrophotometric data of avian retinas is tedious and also requires the sacrifice of many individuals per species (Ödeen et al. 2009). However, sequencing the SWS1 opsin gene can estimate spectral tuning without sacrificing live specimens. The data obtained from sequencing the remaining families could be used to learn more about the evolution of color vision in birds. Also, having this information could alleviate the need to sacrifice rare specimens in studies focusing on how such species may perceive color. Finally, visual contrast studies could be used to continue behavioral research in many areas of avian ecology. For instance, attention is being shifted towards studying aposematic vs. cryptic patterns of animals within avian tetrachromatic color space and how this relates to avian foraging decisions. However, many of these studies have focused on the conspicuousness of vertebrate prey (i.e., Stuart-Fox et al. 2003). Arthropods are a major food source for birds. However there are relatively few studies in the literature that that investigate this phenomenon in arthropods outside the confines of the human visual spectrum.

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1

CHAPTER 3. NOVEL FUNCTIONAL TRAITS CAPTURE THE FUNCTIONAL SPECTRUM OF SPECIES AND DETECT CHANGES IN ECOSYSTEM STABILITY ALONG ENVIRONMENTAL GRADIENTS

3.1 Introduction

Functional diversity, or the range of species' ecological roles in a community, has been investigated in numerous studies in a broad array of taxa. This approach involves classifying species into functional groups based on key ecological traits that define their role in ecosystems and then then using this level of diversity to investigate ecosystem stability. Here I describe two new functional traits to capture the functional spectrum of a species: landscape response and avian visual perception. Landscape response is a trend produced from the relationship between species abundance and landscape pattern measured at ecologically relevant analytical foci. The other, predator visual perception of prey, is a measure of how an avian predator visually perceives its beetle prey. Both of these novel functional traits, never before used in functional diversity studies, are inherent characteristics of species that further define their functional roles in the community. Landscape response is important to consider because individuals' range of movement influences how they interact with their environment (i.e., dispersal, population dynamics, and foraging behavior). Avian visual perception provides a linkage between trophic levels in functional trait space. The incorporation of these traits is also important for capturing how species respond to their environment and interact with their predators,

information that is not easily measured or obtained from the literature. This study is also one of the first that examines whether functional diversity exhibits a threshold response to disturbance. Also, it proposes a new way to examine changes in predator and prey response to habitat fragmentation. Overall, these new methods presented here are highly transferable to other functional diversity studies.

Habitat fragmentation is a primary factor in the decline of biodiversity (Rands et al. 2010) and can be characterized by the isolation of habitats from each other accompanied by habitat loss, the outcome being a mosaic of habitat patches surrounded by non-suitable habitat. Smaller habitat patches have smaller populations that are more susceptible to extinction (MacArthur & Wilson 1967) and isolation decreases the probability of recolonization after local extinction (Fahrig 2003). Additional fragmentation may cause a community to surpass a threshold beyond which there is a sudden change in quality of some aspect of the community or ecosystem (Beisner et al. 2003, Groffman et al. 2006). It has been demonstrated that habitat fragmentation negatively impacts ecosystem function (Didham et al. 1996) and there is empirical evidence that species' loss affects ecosystem processes (Tilman et al. 1996).

Functional diversity, the diversity of traits that determine species' roles or function in an ecosystem (Tilman 2001), measures impacts on ecosystem services more directly than species richness (Tilman et al. 1997, Díaz & Cabido 2001, Heemsbergen et al. 2004, Dang et al. 2005), and consequently is a more direct proxy of change following disturbance (Díaz & Cabido 2001, Ernst et al. 2006) that causes habitat fragmentation. Functional diversity may logically exhibit a threshold response along a gradient that causes species loss if there are redundant species in functional groups. A threshold is a

point where there is a sudden change in some aspect of an ecosystem (Groffman et al. 2006). Once the threshold is passed, the result can be observed as an abrupt change in the response variable (Folke et al. 2004). For instance, several redundant species may be lost with little change in function until the last species occupying a similar trait space is lost. Despite research on changes in functional diversity along gradients of various environmental conditions (de Bello et al. 2005) and habitat degradation (Villéger et al. 2010), little is known about whether functional diversity shows a threshold response to habitat fragmentation considering species with high interaction strength levels (e.g., predators and prey, hosts and parasites). In addition, most studies have used a relatively small number of traits to delineate 'function' or functional groups and such delineation is often done in an aribitrary way, despite the availability of less subjective methods (e.g., Pla et al. 2011). If the ecosystem function of an animal species is to be well-described, variables should include: what it feeds upon, what feeds upon it, details of these inter-trophic interactions, and the 'analytical focus' at which the species operates. Here, I refer to the size to which study grain is aggregated into replicates (sensu Holland & Yang in press) as the analytical focus (hereafter called "focus").

Functional diversity can be measured through different indices (e.g., Petchey & Gaston 2002, Villéger et al. 2008, Laliberté & Legendre 2010) (Figure 3.1). Functional evenness (FEve) and functional divergence (FDiv) were identified by Mason et al. (2005) and further developed by Villéger et al. (2008). Each of these functional diversity measures is an independent measure of functional trait space and describes how species are dispersed within it (Mouchet et al. 2010). Additionally, response diversity measures the heterogeneity of responses among species in a functional group to environmental

change (Elmqvist et al. 2003), and can be quantified with functional dispersion (FDis; Laliberté et al. 2010). Finally, functional redundancy measures the number of species within each functional group (Walker 1992). Both response diversity and functional redundancy have been used to evaluate ecosystem resilience (Bellwood et al. 2003, Laliberté et al. 2010).

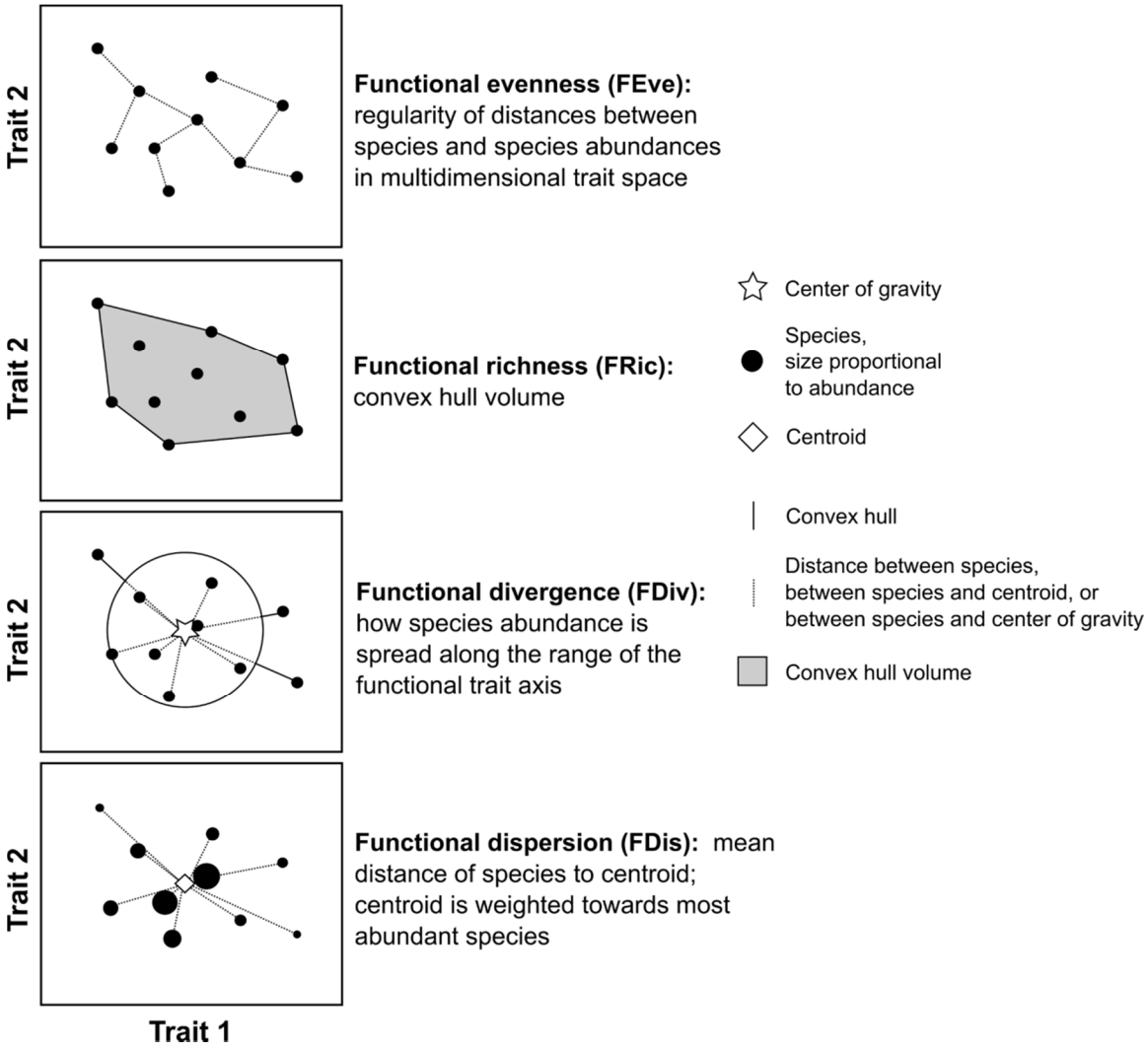


Figure 3.1: Two-dimensional representations of functional diversity indices. FEve, FRic, and FDiv were adapted from Villéger et al. (2008). FDis was adapted from Laliberté & Legendré (2010).

I investigated changes in the functional diversity and response diversity of a multi-trophic community along a habitat fragmentation gradient. The community consisted of wood-boring beetles (Coleoptera: Cerambycidae, the longhorned beetles) and generalist beetles that prey upon wood-borers (Coleoptera: Cleridae, Cucujidae, Histeridae, and Passandridae; Arnett et al. 2002a, b) in a hardwood forest ecosystem. This study is one of the first to investigate insect functional diversity, particularly in beetles. This multi-trophic system is particularly suitable to investigate the existence of a threshold response to habitat fragmentation due to the diverse ecological roles that these beetles have in forests both as larvae and as adults. For instance, the Cerambycidae ("wood-borers" hereafter) contains both pest and beneficial species whose larvae develop in living wood with a particular state of health or deadwood at a particular stage of decay (Hanks 1999, Linsley 1961). Those that feed on deadwood as larvae are important for accelerating wood decomposition (Edmonds & Eglitis 1989, Gutowski 1987), and many adults are pollinators of flowering plants (Kevan & Baker 1983, Linsley 1961). Predacious beetles in some families also utilize wood of a particular condition and depredate prey at different life stages as larvae and adults (e.g., Böving & Champlain 1920). Actually, there is evidence that forest disturbance impacts the abundance of some families of wood-borers differently than their predators (Ryall & Fahrig 2005, Costa et al. 2013). For instance, *Thanasimus dubius*, a clerid predator, was found to disperse farther than its wood-borer prey but, unlike its prey, was restricted to pine forests (Costa et al. 2013). Furthermore, isolated habitats contain a greater proportion of wood-borers than to beetle predators (Ryall & Fahrig 2005). Also, it has been previously observed that wood-

borer abundance may be higher in herbaceous fringes rather than forests (Wermelinger et al. 2007).

Although previous studies have shown how disturbance affects the functional diversity of multi-trophic systems (Lavorel et al. 2013, Moretti et al. 2013, Deraison et al. 2015, Lefcheck & Duffy 2015), they have not taken into account the ecological roles of species with respect to inter-trophic interactions between predators and prey. I also considered the effects of a third tophic level: avian predators of both wood-borers and predatory beetles. Insects including forest beetles are consistently depredated by birds (Jones 1934, Recher & Majer 2006, Remmel et al. 2011, Flower et al. 2014). Insects are known to use aposematic (Jones 1934) or camouflage patterning (Kettlewell 1955) to minimize detection (and consequently mortality) by insectivorous birds. Yet birds use multiple (direct and indirect) cues to detect insects (Lyytinen et al. 2004, Olofsson et al. 2010) against various backgrounds with different success rates (Mand et al. 2007). The interplay between detectability of beetles by avian predators and the potential consequences for the mortality of wood-borers and predatory beetles has not been taken into account in the literature despite its major ecological implications (Stevens 2007). I addressed this gap by considering for the first time in the delineation of trait space how predators (i.e., birds) perceive prey (i.e., beetles).

I also considered an additional novel trait, landscape response trend, since the scale at which species respond to landscape pattern is known to influence dispersal, population dynamics, foraging behavior, among other processes (Addicott et al. 1987, Dunning et al. 1992). Different species respond to different phenomena within differently sized ecological neighborhoods, or with different magnitudes of response at a

wide range of foci. My landscape response trend variable is a nominal class variable that groups species together according to the similarity in their overall response–foci profile.

I used the functional groups within the wood-borer – predator beetle community to see if the often-cited hypothesis that habitat fragmentation has a greater negative impact on predators than on prey would apply to the functional diversity of wood-boring beetles and the predacious beetles that attack them (Thies & Tscharntke 1999, Ryall & Fahrig 2005, Costa et al. 2013). Functional diversity may exhibit a threshold response considering that species loss within functionally redundant functional groups would not be marked by ecosystem change until a certain number of species, or the last species occupying a similar trait space is lost. I therefore predicted that functional diversity would have a threshold response to habitat fragmentation because of the functional redundancy within my functional groups. I also expected that landscapes with greater habitat fragmentation would harbor beetle communities with a lower response diversity and functional redundancy (Laliberté et al. 2010).

3.2. Methods

3.2.1 Beetle collection

Wood-borer beetles (Cerambycidae) and their beetle predators were sampled at 25 sites along a forest fragmentation gradient in Indiana, USA (Figure 3.2). The forest habitat was secondary growth forest fragmented by agricultural and urban land use. The range of the fragmentation gradient measured at a 2 km radius was from 100% to

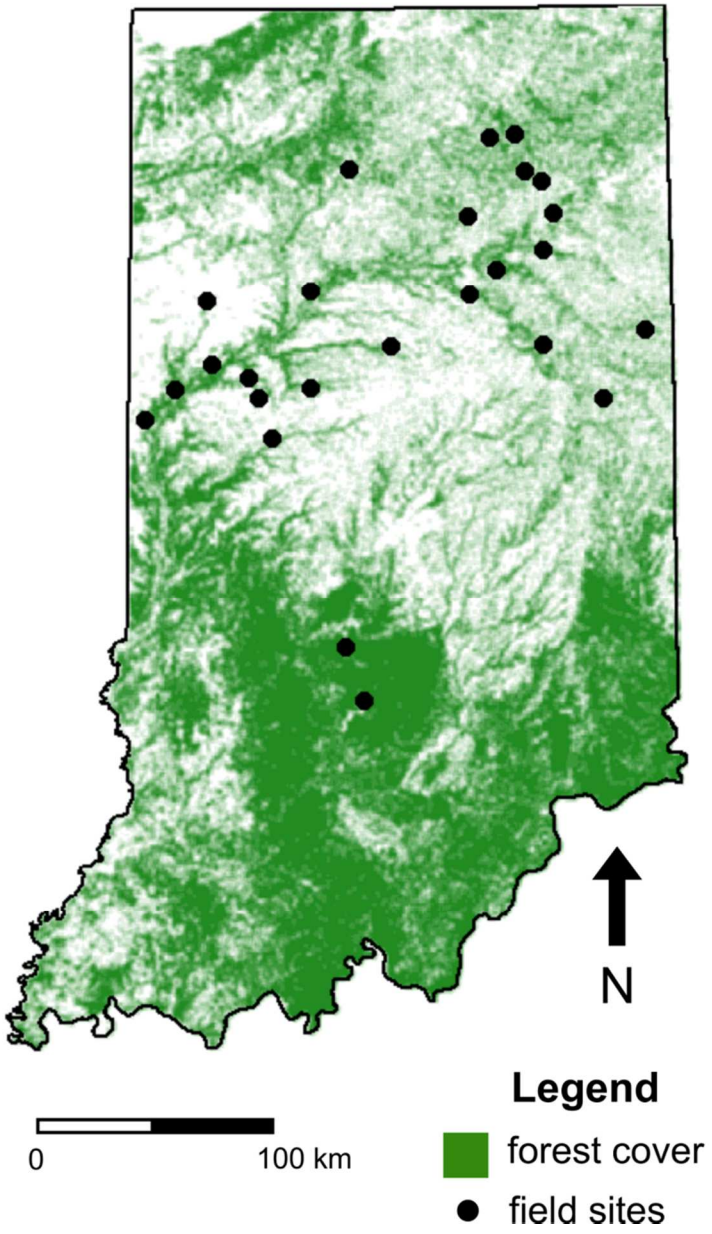


Figure 3.2: Field sites selected along a gradient of forest fragmentation in the state of Indiana, USA.

approximately 5% forest. Within each site, beetles were trapped using one Lindgren multiple funnel trap (12 funnel size; Phero Tech, Delta, Canada), one Intercept panel trap for bark beetles (Integrated Pest Management Tech, Portland, OR), and one multi-pane window trap, all baited with 99% ethanol to trap beetles (Holland 2006). Trapping lasted

70 – 90 d over the summer of 2006 and 2007. Wood-borers were identified to species using Yanega (1996), Linsley (1962a, b, 1963, 1964), Linsley & Chemsak (1972, 1976), Arnett et al. (2002a, b) and Downie & Arnett (1996a, b). I re-examined trap residues in 2013 to obtain the predacious beetle data. I identified all specimens in the families Cleridae, Cucujidae, Histeridae, and Passandridae using keys in Arnett et al. (2002a, b) and Downie and Arnett (1996a, b). All specimens were deposited into the Landscape Ecology and Biodiversity laboratory at Purdue University.

3.2.2 Landscape data (#1 in Fig. 3.3)

Forest fragmentation was characterized at each site using 31 landscape metrics at 12 foci 90 m – 7.29 km on a binary forest/nonforest map reclassified from NLCD 2006 data in GRASS GIS (GRASS Development Team. 2012; Appendix C). These metrics are standard measures similar to those found in FRAGSTATS. To select landscape metrics that did not covary, I calculated the Euclidean distance matrix between landscapes based upon standardized fragmentation measures at the sites using the vegan package in R (Okansen et al. 2013) and subjected this to Ward's clustering. This was repeated at each focus. The cluster analysis grouped similar indices at each focus. Scree plots were used to determine pruning heights. I selected the metric from each resulting cluster that best improved model significance of the subsequent redundancy analysis (#2 in Fig. 3.3) or multiple regression (see below) (#4 in Fig. 3.3) to represent the landscape gradient.

3.2.3 Functional traits (Table 3.1, #1 – 3 in Fig. 3.4)

I defined functional traits for each beetle species as those attributes that best describe species' roles in the community. I characterized the life history, habitat, and hosts of each species by compiling data from the published literature (#1 in Fig. 3.4, Table 3.1, Appendix A, B). Variables included adult size, part of tree larvae develop within (e.g., branch, stem), layer of wood larvae develop within (e.g., bark, cambium, xylem), host wood condition (e.g., under stress, dead but sound, decayed), family of host tree (one to many of dozens of tree families), number of tree families used (a measure of specialization). I included the taxonomic subfamily and tribe because I assume this will account for some biological traits not included or possibly not even measurable due to phylogenetic relationships. I included a novel trait that classifies the nature of how a species' response to landscape changed with scale (Yang 2010) as an important dimension of their ecological role (#2 in Fig. 3.4). The landscape data measured above were subjected to principle component analysis and the site scores along the first principle component at each focus were correlated to the species abundance at the sites. This was preferred to correlating to any one landscape metric because the landscape metrics were highly correlated. I correlated the first principal component (λ=0.6, representing both habitat area and patch interspersion) and species abundance data with a Spearman's rank test and then plotted the absolute value of the Spearman's ρ across scales. A forward stepwise ANOVA was used to determine whether higher order polynomials were justified to describe the relationship of $|\rho|$ vs. scale. The nature of the response trend (e.g., linear, second-order) was used as one functional trait for each species.

Table 3.1: Functional traits selected to capture the functional spectrum of beetles in hardwood forests. Traits were obtained from literature, directly measured (M) or calculated (C). New traits developed here include "landscape response trend" and "avian visual perception."

Cerambycid Functional Traits		Number of Categories			Predator Functional Traits
Mean size (mm)					Mean size (mm)
Taxonomy (Subfamily + Tribe)		32	10		Taxonomy (Subfamily)
Resemblance		3	3		Resemblance
Avian visual perception	M	9	6	M	Avian visual perception
Flight activity duration		9	8		Flight activity duration
Landscape response trend (LSR)	C	3	3	C	Landscape response trend (LSR)
Host tree condition		5	3		Habitat tree condition
Larval wood type		5	5		Habitat tree type
Diel activity		3	2		Larval habitat
Larval feeding behavior (part + layer)		8	5		Larval feeding behavior
Adult feeding behavior		6	2		Larval cannibalism
Diet breadth		3	4		Adult feeding behavior
Number host families attacked			6		Adult habitat
Number host genera attacked			8		Body shape
Host families		42			

To assess how wood-borers and predatory beetles are perceived by avian predators (# 3 in Fig. 3.4), I used a perceptual modeling approach (Endler 1990, Vorobyev & Osorio 1998, Endler & Mielke 2005) widely accepted in the behavioral and sensory ecology literature (e.g., Kemp et al. 2015). The rationale behind this approach is that avian visual perception is different from that of humans because of the presence of

an extra cone photoreceptor type (ultra-violet- or violet-sensitive), organelles that filter the light before reaching the visual pigments (i.e., oil droplets), and different absorbance properties of the ocular media (Cuthill 2006). Consequently, perceptual models estimate how conspicuous an object is from the perspective of the background under a given set of ambient light conditions and from the perpective of a given visual system (Endler 1990). Perceptual models yield a visual contrast value (i.e., the higher the value the higher the degree of conspicuousness) in both the chromatic and achromatic dimensions (i.e., chromatic and achromatic contrast, respectively; Vorobyev & Osorio 1998). Therefore, I calculated the chromatic and achromatic contrasts of dorsal beetle patterns against various backgrounds that occur where predators may find them such as tree bark. I also conducted similar visual contrast calculations comparing the beetles to a 'background' of several species of aposematic wasps that are common in the study area to incorporate the effect of mimicking wasps on predation by birds. I used all visual contrasts calculated through this approach. Details on the perceptual model calculations and how they were incorporated into my functional trait analysis are given in Appendix D, Appendix E, and Appendix F.

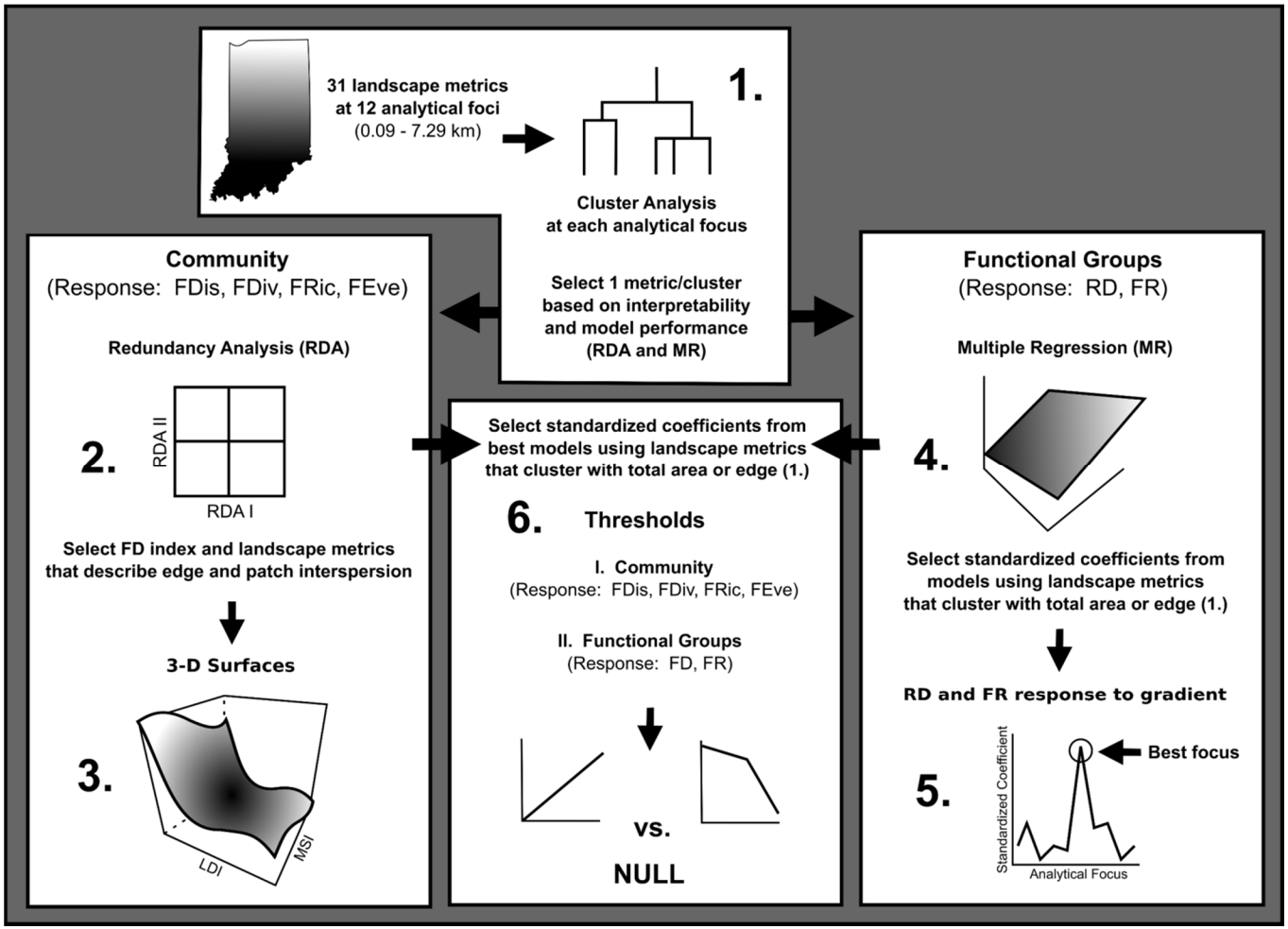


Figure 3.3: Flowchart outlining methods to assess changes in functional diversity along the fragmentation gradient. I examined how functional diversity changed, including whether functional diversity displayed a threshold change, along the gradient at community and functional group levels.

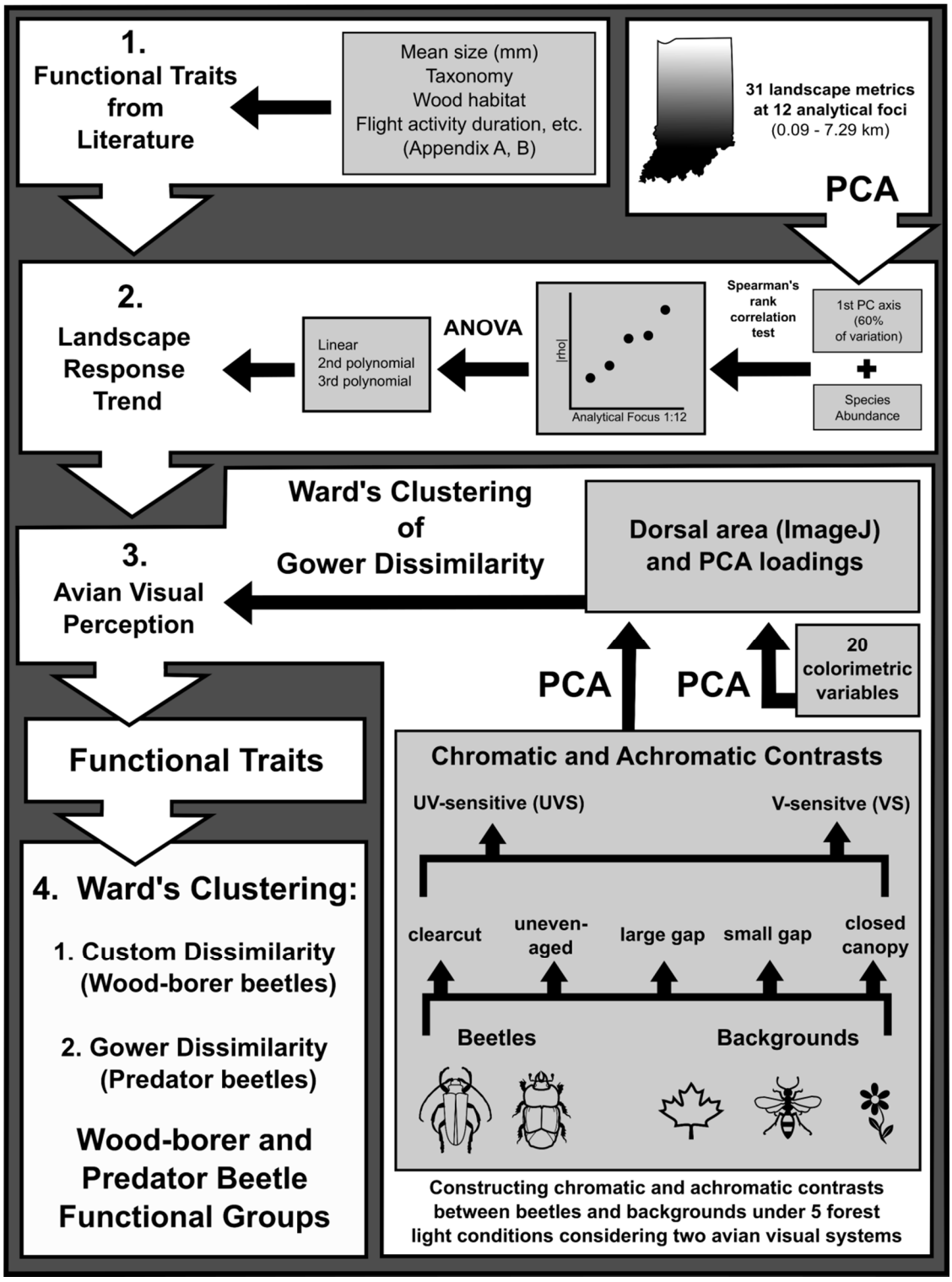


Figure 3.4: Flowchart outlining methods to obtain functional groupings of beetles. Methods include the collection of all functional traits used to categorize wood-borer and predator beetles into functional groups.

3.2.4 Functional groupings (#4 in Fig. 3.4)

I used a total of 17 traits of wood-borers and 14 traits of predator beetles (Table 3.1, Appendix A, B) to classify species into functional groups. All wood-borer traits except for one, larval host condition, were weighted so that all conditions within each trait summed to one (Laliberté & Legendre 2010). I considered *a priori* that larval host condition should be double-weighted so that the host conditions summed to two because these beetles spend most of their lives as larvae (Linsley 1961) and much of their roles in forest ecosystems revolve around the condition of the host tree (Hanks 1999). All non-continuous variables were treated asymmetrically. However, for one wood-borer trait, host family, I had 42 conditions. I wished to compare species so that double zeros are not counted as matches for this trait, but considering the number of conditions, its summed weight would not approach the desired total weight of one. To circumvent this problem, I created my own dissimilarity by using the FD package in R (Laliberté & Legendre 2010, Laliberté & Shipley 2011) to calculate Gower dissimilarity of all wood-borer traits except host family and then using the vegan package in R (Okansen et al. 2013) to calculate Jaccard's dissimilarity of the trait tree 'host family.' The Gower dissimilarity matrix and the Jaccard's dissimilarity matrix were multiplied by the fraction of traits they contained, and these products were summed to obtain the final dissimilarity matrix for the wood-borers. Gower dissimilarity was calculated for all predator functional traits. The Gower measure was most appropriate because I had multiple variable types (continuous, ordinal, and categorical) and missing values (Gower 1971, Legendre & Legendre 1998, pp. 258–260). Ward's minimum variance clustering method on dissimilarity was computed from all functional traits (Pla et al. 2011). To determine pruning height for the

wood-borer dendrogram and thus delineate functional groups I used k-means clustering to plot within groups sum of squares by number of clusters k (Legendre & Legendre 1998, pp. 359–355). Scree plots for predators were used to determine dendrogram pruning heights.

Functional diversity (FD) indices that describe how species abundances are dispersed in multidimensional trait space were calculated using the FD package in R (Laliberté & Legendre 2010, Laliberté & Shipley 2011) at the community level for wood-borer and predator beetles. I included indices of functional dispersion (FDis), functional divergence (FDiv), functional richness (FRic), and functional evenness (FEve) (Villéger et al. 2008, Laliberté & Legendre 2010). I used the Cailliez correction method since my species-species distance matrix could not be represented in Euclidean space. Details may be found in the FD package (Laliberté & Legendre 2010, Laliberté & Shipley 2011) and in Cailliez (1983).

3.2.5 Gradient analysis (Figure 3.3)

I selected eleven of twelve radii that correspond to 0.15 km – 7.29 km radii to conduct all gradient analyses (Appendix C, Table C.1). Since it is already known that species in my dataset respond to the landscape at different foci (Yang 2010), functional diversity may also respond at different foci. Therefore, I considered it important to perform my analysis at multiple foci to be able to best capture the relationship between beetle functional diversity and changes in forest landscape pattern.

3.2.5.1 Community (RDA, #2 in Fig. 3.3)

I conducted RDA at each focus to examine whether habitat fragmentation has a greater negative impact on predator beetle functional diversity than wood-borer functional diversity due to predator beetle species' increased sensitivity to disturbance. I used permutation tests to test the strength of the relationship between the functional diversity indices (FRic, FEve, FDiv, and FDis) and the landscape metrics.

3.2.5.2 Three dimensional surface of functional richness (#3 in Fig. 3.3)

I selected two different landscape metrics to describe fragmentation in the landscape, one measuring patch interspersion (landscape division index, LDI) and another measuring patch shape complexity (mean shape index, MSI). I selected these because they met the following criteria among wood-borer and predator RDA triplots: 1) the relationship between landscape and functional diversity from the RDA triplots must be significant at the same focus, and 2) the same two metrics describing habitat fragmentation must be correlated with any given functional diversity index. Given that they met these criteria, the three-dimensional (hereafter, 3D) plots produced of wood-borer and predator community functional diversity could be comparable. Furthermore, assessing fragmentation by separate measures in a landscape at a given scale is important because habitat fragmentation affects populations in different ways. For instance, decreased patch area and increased patch isolation may reduce species persistence in the landscape (Fahrig 2003). Also, edge effects may negatively impact populations by 1) increasing the time species spend in non-patch habitat (Fahrig 2002), 2) causing negative species interactions (Chalfoun et al. 2002), or 3) because species have varying

sensitivities to edge (Costa et al. 2013). Here, LDI and MSI were both correlated with FRic of both beetle groups at the same focus (0.81 km) in the RDA analysis. LDI and MSI were used in polynomial regression with FRic. The difference between standardized predicted values within wood-borer FRic and predator FRic was plotted against LDI and MSI to obtain a 3D surface which allowed me to compare how overall community functional diversity changed with landscape fragmentation.

3.2.5.3 Functional groups (#4 – 5 in Fig. 3.3)

To test the prediction that greater habitat fragmentation will cause a decrease in response diversity and functional redundancy within beetle communities (Laliberté et al. 2010), I used multiple regression to test the relationship between 1) functional redundancy and 2) response diversity with the landscape metrics (#4 in Fig. 3.3). I measured functional redundancy (FR) as the number of species within each functional group. I used FDis weighted by species abundance for each functional group as a measure of response diversity (RD). I removed traits within functional groups that had values for <50% of the species (Laliberté et al. 2010) when calculating FDis. Box-Cox transformations were used to prepare response measures that did not meet normality assumptions (Venables & Ripley 2002). I then selected the standardized coefficients from multiple regression models of functional redundancy (FR) and response diversity (RD) with the landscape measures that were representative descriptors of habitat area and edge. Following a similar approach used to construct the 3D surfaces, I chose to assess fragmentation by separate measures because habitat fragmentation affects populations in different ways. Because no specific measure of habitat area or edge was used for all

models, I selected the two landscape metrics that clustered with either total area or edge density (#1 in Fig. 3.3). These coefficients were plotted at each focus (#5 in Fig. 3.3, Appendix G). I considered the focus/radii with the coefficient with the greatest magnitude the most appropriate for reporting significance of relationships between FR and RD and landscape pattern.

Functional traits are often considered to be response traits, traits that measure species' response to disturbance, or effect traits, traits determine species' effects on one or multiple ecosystem functions (Suding et al. 2008). Laliberté et al. (2010) used only response traits (traits that measure species' response to disturbance) to calculate FDis as their measure of response diversity of plant communities. Changes in plant functional diversity have been investigated in many studies (recently, Laughlin et al. 2015, Mandle & Ticktin 2015), and much previous work has further classified traits into response and effect traits for these organisms (see Suding et al. 2008). Unlike those commonly used for plants, the beetle species traits that I used to define their ecological roles do not fall into clear categories such as response and effect. Given the breadth of the functional traits I selected to discriminate the ecological roles of beetles, I believe that changes in FDis for a given functional group calculated from all traits served as a strong indicator of a group's resilience to disturbance. Thus, I used FDis calculated at the functional group level as a measure of response diversity to test my prediction that greater habitat fragmentation would lead to a decrease in response diversity and functional redundancy within beetle communities (Laliberté et al. 2010).

3.2.5.4 Threshold response (#6 in Fig. 3.3)

I aimed to test the prediction that functional diversity has a threshold response to habitat disturbance. I assessed the changes in functional diversity with fragmentation at both the community and functional group level and whether these changes were marked by a threshold response. I selected the following from the RDA and multiple regression models that explained the greatest proportion of variance (Appendix H): two landscape metrics (one representing habitat area, the other, the amount of edge) and the response variables from these models. The response variables included the functional diversity indices (Figure 3.1) assessing wood-borer and predator community-level functional diversity and functional redundancy and response diversity of each functional group. As before, because no specific measure of amount of habitat area or amount of edge was used for all RDA (community level) and multiple regression (functional group level) models, I selected the two landscape metrics used in the previous RDA or multiple regression models that previously clustered with either total area or edge density (#1 in Fig. 3.1). The relationship between 1) the community-level functional diversity indices, 2) FR, and 3) RD of functional groups and these metrics was examined with linear and segmented regression with the segmented package in R (Muggeo 2003, Muggeo 2008). I created null models by randomizing values within response variables using the picante package in R (Kembel et al. 2010). I compared these models and chose the best relationship (linear, threshold, or null) based on lowest AIC scores of these models. In this study, a threshold response of functional diversity was indicated by the segmented regression model having the lowest AIC score. I then further examined the significance and point of change in these segemented regression models with the lowest AIC scores.

3.3 Results

3.3.1 Functional groupings (Figure 3.5)

A total of 81 species of wood-borers and 24 species from the four predatory beetle families were collected. Cluster analysis on ecological traits revealed three wood-borer functional groups and two predator beetle functional groups (Fig. 3.5, Appendix I). I defined discriminating traits to characterize functional groups as those traits that were present in >50% of the species within the functional group, illustrated in Figure 3.5. One of my novel traits, landscape response trend, was a discriminating trait of FG2, and many members of FGA belonged to avian visual perception category 1, one of ten possible categorical appearances to birds.

3.3.2 Community (RDA analyses, triplots shown in Appendices J and K)

Wood-borers and predators responded to the fragmentation gradient differently, but contrary to my hypothesis, wood-borer functional diversity rather than predator functional diversity was more sensitive to fragmentation. Functional diversity of wood-borers responded strongest to changes in the landscape within a 4.05 km radius (df=3, F=4.92, p=0.005) and at 7.29 km (df=3, F=3.44, p=0.005). Predator functional diversity had the strongest response to fragmentation at radii of 5.67 km (d.f.=3, F=2.51, p=0.005) and 7.29 km (df=3, F=2.77, p=0.005). Among the functional diversity indices, functional richness (FRic) of both groups had the strongest correlation with the landscape, but wood-borer FRic was decreased while predator FRic was increased in fragmented landscapes. FDis, FDiv, and FEve of both communities had weak correlations with the landscape.

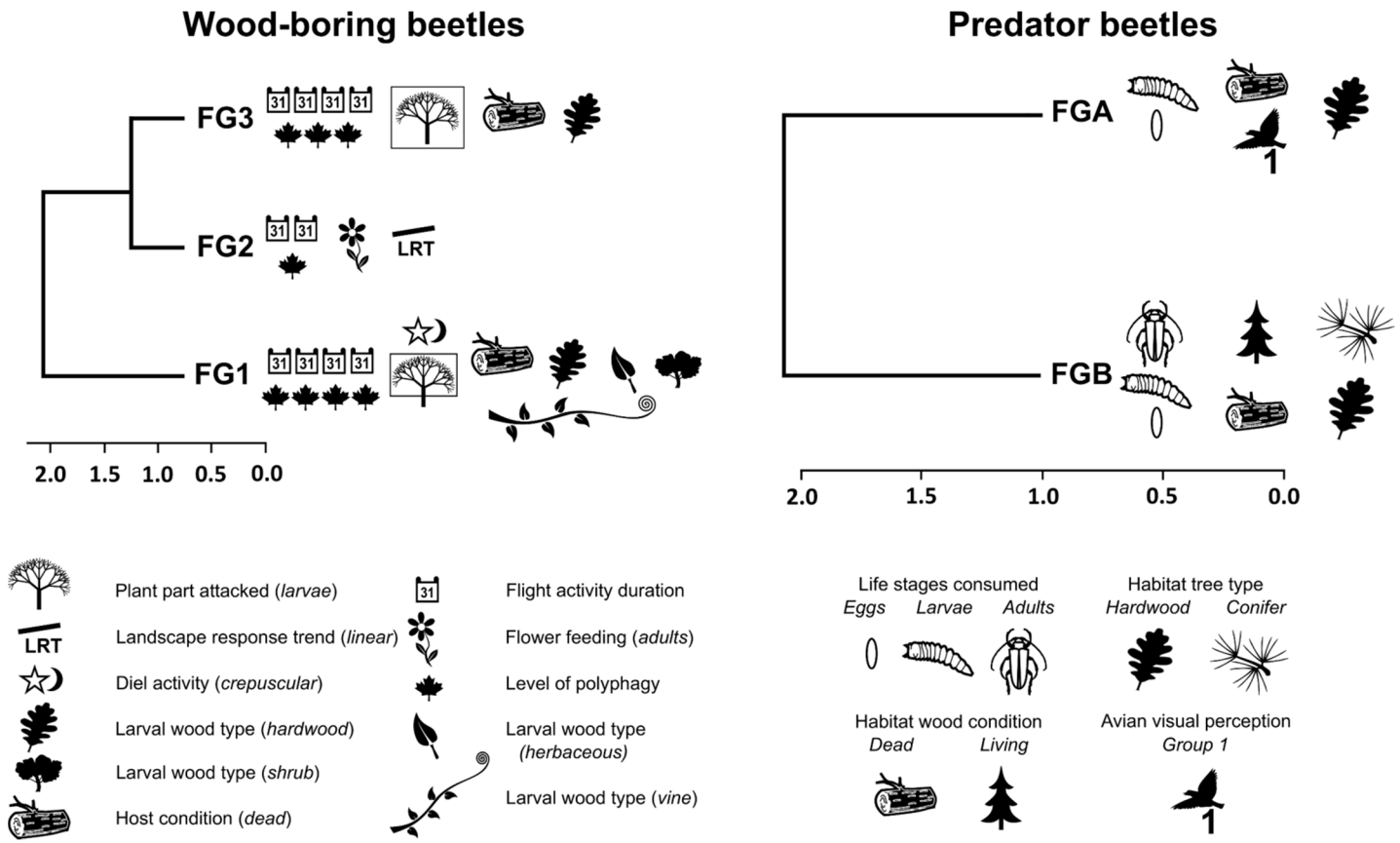


Figure 3.5: Dendrogram depicting three wood-borer functional groups and two predator functional groups. Icons represent discriminating traits that were present in >50% of the species within the functional group.

3.3.2.1 3D surface of functional richness (Fig. 3.6)

Overall, community functional richness was greatest in intact forest landscapes. The 3D surfaces revealed that wood-borer and predator FRic had different responses to patch interspersion. Similar to the RDA results, wood-borer FRic was decreased while predator FRic was increased in fragmented landscapes. Furthermore, predator functional richness was increased in habitats with greater edge complexity.

3.3.3 Functional groups (Fig. 3.7, Appendix G)

I found support for the prediction that functional redundancy (FR) and response diversity (RD) would decrease with fragmentation, at least for the majority of the functional groups. Generally functional redundancy and response diversity were reduced in fragmented landscapes. However, response diversity of FG2 increased with amount of habitat edge, and the correlation between 1) functional redundancy and 2) response diversity of FGA was not significant with landscape pattern. Although not examined specifically, I found that only FG2 had all species missing at some of the sites.

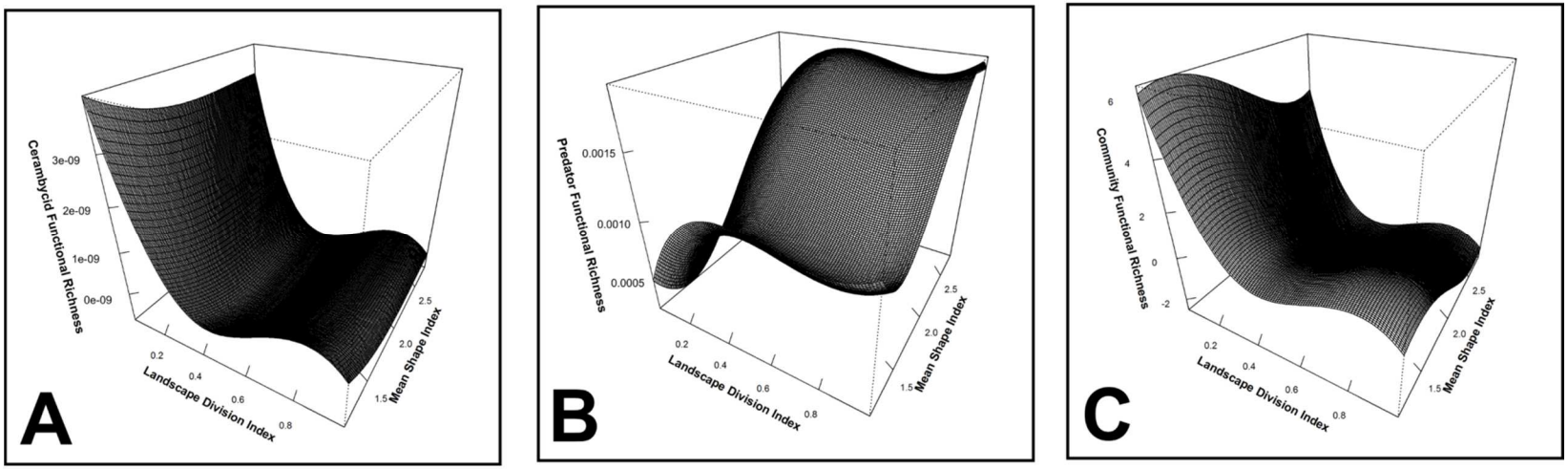


Figure 3.6: Three-dimensional curves that represent change in functional richness (FRic) of beetle communities along two aspects of landscape pattern, patch interspersion (landscape division index, LDI) and patch shape complexity (mean shape index, MSI). A. Wood-borer FRic. B. Predator FRic. C. Community FRic.

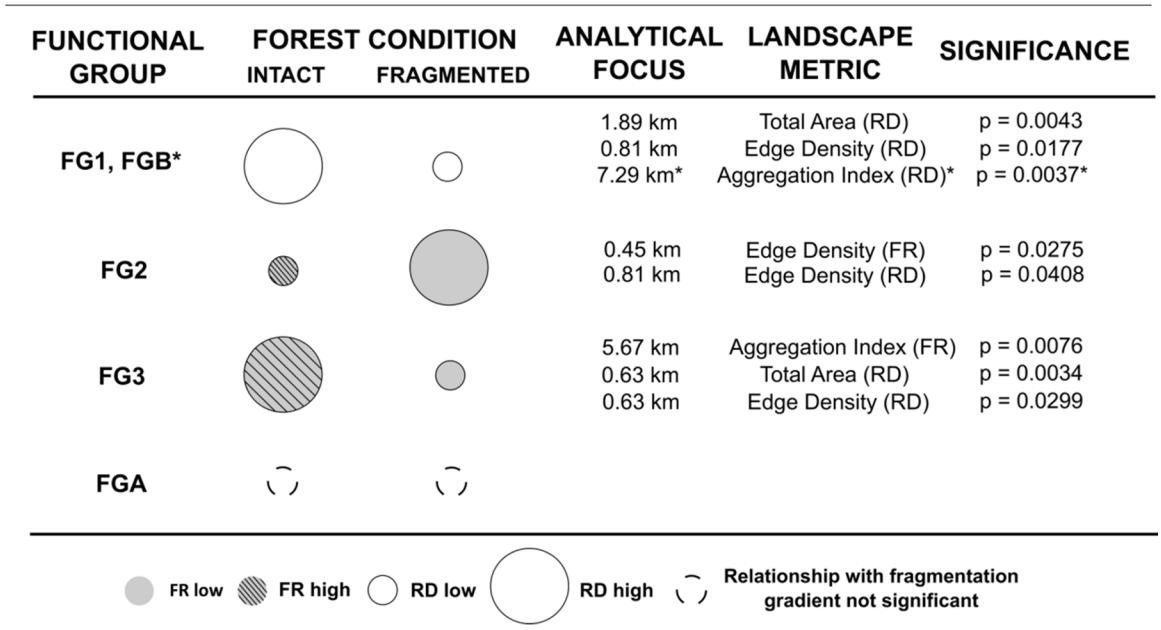


Figure 3.7: The relationship of functional redundancy (FR) and response diversity (RD) of wood-borer and predator functional groups with fragmentation.

3.3.4 Threshold response (Table 3.2, Fig. 3.8)

I predicted that functional diversity will have a threshold response to habitat fragmentation. This prediction was supported by segmented regression models of wood-borer FDis, Eve, and FRic and predator FDis and FDiv with the landscape having the lowest AIC values. Functional redundancy (FR) of all functional groups except FGA had a threshold response to fragmentation. However, out of the segmented regression models having the lowest AIC scores, only the relationships between predator community FDis and predator FGB FR with landscape were significant (Fig. 3.8). In these relationships, predator community FDis suddenly decreased in landscapes with larger forest area of approximately 43.8 hectares. Furthermore, functional redundancy of FGB suddenly increased in habitats with more convoluted edges (mean shape index of 1.78). No

Table 3.2: Best model selection (in bold) for wood-borer and predators at the community and functional group levels. "NA" for FGA signifies that the segmented model examined at a focus of 0.81 km did not have the lowest AIC score.

	Wood-borers Focus 10 (4.05 km)				**Predators** Focus 6 (0.81 km)	
Community	**FDis**	**FEve**	**FEve**	**FRic**	**FDis**	**FDiv**
Linear	-457.49	-77.28	-87.00	-117.22	-287.20	-14.50
Threshold	**-458.80**	**-79.93**	**-89.38**	**-117.92**	**-292.14**	**-18.43**
Null	-455.28	-79.35	-76.86	-113.42	-287.97	-15.67
Landscape metric	Frac.	Agg.	Frac.	Agg.	Area	Edge
Degrees of freedom	21	21	21	21	21	21
t-value	1.064	0.874	0.922	0.241	2.145	0.559
p-value	0.3	0.392	0.367	0.812	**0.044**	0.582
Functional Redundancy (FR)	**Focus 6 (0.81 km)** **FG1**	**FG1**	**FG2**	**Focus 11 (5.67 km)** **FG3**	**Focus 6 (0.81 km)** **FGA**	**Focus 12 (7.29 km)** **FGB**
Linear	-86.60	-82.13	76.31	30.33		77.27
Threshold	**-89.91**	**-82.17**	**76.05**	**29.10**		**76.87**
Null	-81.55	-82.14	80.68	32.44		86.18
Landscape metric	Agg.	Edge	Patch	Agg.	**NA**	Shape
Degrees of freedom	21	21	21	21		21
t-value	-0.440	-0.468	-0.158	0.132		-3.173
p-value	0.664	0.646	0.876	0.896		**0.005**

Area: Total area
Agg.: Aggregation index
Frac.: Mean fractal dimension index
Edge: Edge density
Patch: Mean patch area
Perim.: Mean perimeter area ratio
Shape: Mean shape index

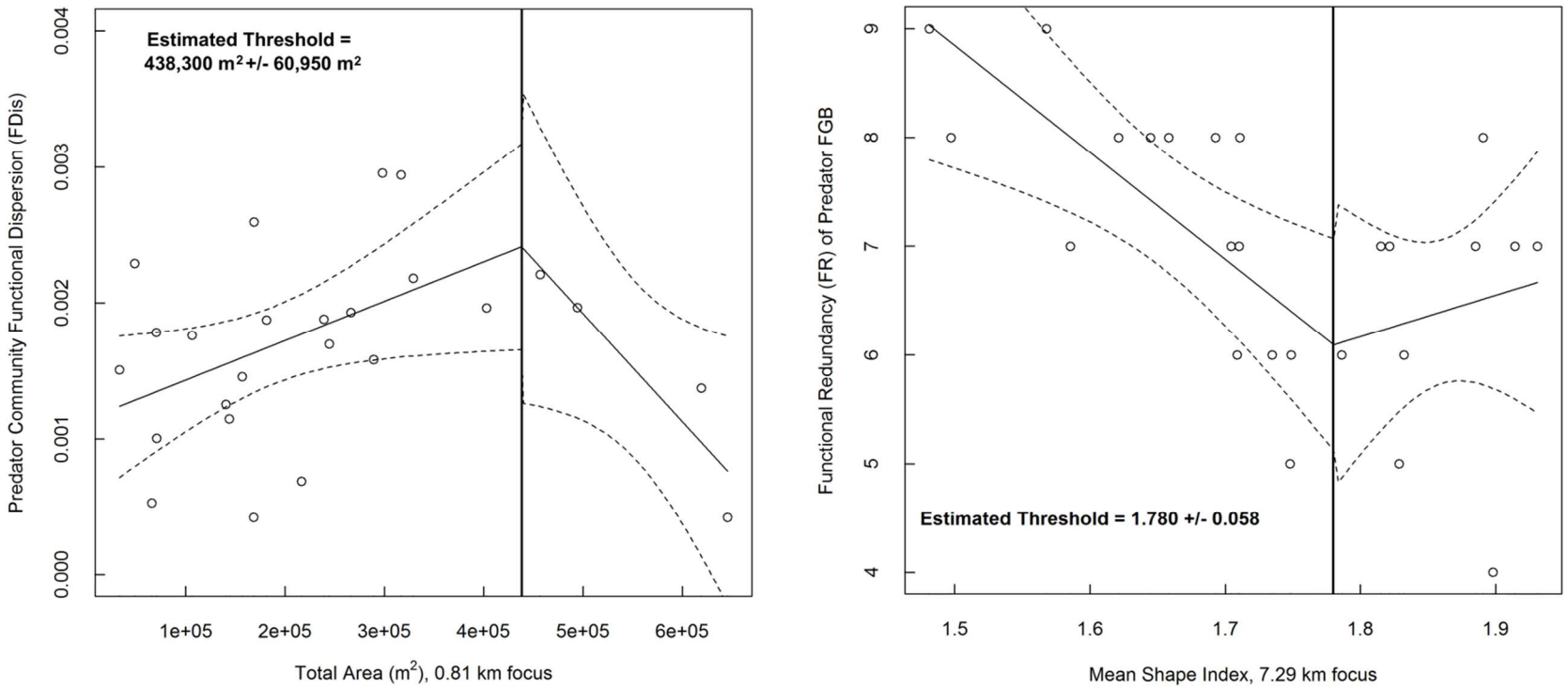


Figure 3.8: Threshold responses of predator community functional dispersion (FDis) to total area ($p = 0.0397$) and functional redundancy (FR) of predator FGB to mean shape index ($p = 0.00458$).

functional groups' response diversity (RD) showed a threshold response to fragmentation.

3.3.5 General comments

Overall, I found that at the community level functional diversity of wood-borers represented by functional richness was more negatively impacted by fragmentation than predator beetle functional diversity. However, response diversity and functional redundancy of wood-borer and predator functional groups were generally reduced in fragmented landscapes. Furthermore, functional diversity, assessed at both community and functional group levels, displayed a threshold response to fragmentation. This threshold response suggests that the community maintained a stable state along the gradient but at a threshold point suddenly began to change.

3.4 Discussion

My assessment of functional diversity along a fragmentation gradient is unique among functional diversity studies. First, I included all known ecological information about the beetle species and developed two novel functional traits that further incorporate such dimensions as dispersal and the multitrophic interactions between beetle prey and avian predators. Overall, these functional traits produced functional groups that captured a complete spectrum of the beetle's functional roles in temperate hardwood forest ecosystems based on current ecological knowledge of these groups. I then examined changes in functional diversity of this multitrophic community with habitat fragmentation using these functional groupings. Since species respond to changes in the landscape

pattern differently, this species-level response may translate to similar responses at the functional group level. I therefore compared changes in functional diversity across the range of ecologically relevant foci. In addition, I developed new methods to produce 3D surfaces of functional diversity to examine changes in trophic levels simultaneously along the fragmentation gradient. Also unique to this study, I investigated whether functional diversity exhibits a threshold response to habitat disturbance.

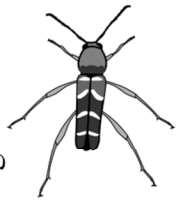
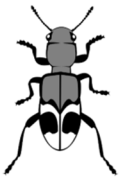
I expected that predator functional diversity would have demonstrated a greater sensitivity to edge and patch isolation than the wood-borer functional groups. My logic was based on the following studies. Costa et al. (2013) found that predator beetles are more sensitive to habitat edges (Costa et al. 2013) and are lower in abundance in isolated stands relative to the abundance of their prey (Ryall & Fahrig 2005). Considering that functional groups with a greater number of species are more likely to share more diverse functional traits between them (Tilman et al. 1996) and that dominant species can have more diverse trait profiles (Walker et al. 1999), I predicted that fewer, less abundant predator species in fragmented forests would result in decreased functional diversity. However, at the community level, predator functional richness was increased while wood-borer functional richness was decreased in fragmented landscapes. I did not assess community change at the species level since previous studies have already made such comparisons in other systems (e.g., Villéger et al. 2010, Baraloto et al. 2012), but I propose that discrepancies between this and the previous studies on wood-borers and their beetle predators are due to the assessment of different levels of diversity (species vs. function). For instance, one scenario that would result in different patterns between species diversity and functional diversity would be in functionally redundant

communities. These communities may harbor high species diversity, but if there is high functional redundancy among species in the community, functional diversity would be low. Regarding my study functional richness was measured by the volume of multidimensional trait space and is obtained from the traits of the species present in the community. Functional richness may be high even if few species are present, as long as those species have diverse trait profiles.

In accord with my predictions, I found that wood-borer and predator functional groups (except predator FGA) had reduced functional redundancy and/or response diversity with forest fragmentation. Low functional redundancy could decrease the resilience of the community to disturbance leading to reduced ecological function. For instance, Bellwood et al. (2003) found that out of the 35 species of parrotfish observed in their study, one was principally responsible for performing the function of bioerosion of coral. Bioerosion is a critical process that forms the physical structure of the coral community structure by reducing the calcium accumulation rates of the reef (Bellowood et al. (2003). This parrotfish species is likely a keystone species, being a principal driver of a coral community's physical structure (Bellwood et al. 2003). Population densities of this parrotfish were very low, which the authors concluded could impair normal ecosystem function resulting in a loss of resilience in that system. Specific to my system of wood-borers and predator beetles, despite this loss of resilience due to reduced functional redundancy and/or response diversity of the beetle functional groups, only the wood-borer FG2 had all species missing at some of the sites. Interestingly, wood-borer FG2 had the lowest functional redundancy out of all of the other functional groups which was further reduced in fragmented landscapes (Table 3.3). I propose that this reduced

functional redundancy lowered the group's resilience to habitat change which contributed to the group being missing at some of the sites.

Table 3.3: Number of species (functional redundancy) within each functional group. Species cannot be classified within multiple functional groups.

	Functional Group	# Species/ Functional Group
Longhorned beetles 	**FG1**	28
	FG2	8
	FG3	45
Predators 	**FGA**	13
	FGB	11

I also found that functional diversity assessed at both the community and functional group levels of wood-borers and their predators exhibited a threshold response to fragmentation. Specifically, I found that functional redundancy (FR) of all functional groups (except predator FGA) had a threshold response. Even though the segmented regression was selected as the best model in the above comparisons, only the relationships of the predator community's FDis and the FR of predator FGB with the landscape were significant. Predator FDis, or the mean distance of species to the

centroid, suddenly decreased with a forest area of approximately 43.8 hectares whereas the number of species within FGB suddenly increased with patch shape irregularity (Fig. 3.8). No functional groups' response diversity (RD) displayed a threshold response to fragmentation.

An important result of this work is that functional diversity, like species, responds to disturbance at different foci (Figure 3.7, Appendix G, J, K). My assessment of change in functional diversity across the gradient of habitat fragmentation was with models that included predictors consisting of landscape pattern measured at the most explanatory focus. These analyses were conducted at the community and functional group levels for wood-borers and predator beetles. This approach allowed me to avoid a type 2 error of erroneously retaining a false null hypothesis. If functional diversity was assessed with a single predictor assessed at a single focus, I would have not detected many of the significant responses of functional diversity to landscape pattern.

Such differences in response to landscape pattern at a particular focus may relate to the functional groups' discriminating traits (Figure 3.5). For instance, functional redundancy, or the number of species, of FG2 was reduced with habitat fragmentation at a smaller focus (Figure 3.7) which would indicate that species' dispersal and use of complementary habitats is limited in fragmented landscapes (Addicott et al. 1987). Traits discriminating FG2 that could reduce these abilities include having few known larval host plants and a short flight period (Figure 3.5). However, functional redundancy was reduced with habitat fragmentation at a larger focus (Figure 3.7). FG3 was discriminated by larvae having a wide range of host plants that also feed on more parts of trees and shrubs (Figure 3.5). A wider range of functional roles possessed by FG3 may enable

species within this group to utilize complementary habitats, and thus be more tolerant of fragmentation at local and intermediate foci. The outcome of these findings demonstrates that ecologically relevant information on the response of functional diversity to disturbance may not be captured if functional diversity is assessed at a single focus.

Obtaining 3D surfaces of FD indices could be an approach for determining appropriate landscape configurations for maximizing functional diversity among single or multiple communities. In my study, the 3D surfaces (Figure 3.6) were constructed at a focus of 0.81 km at which I presume many of the beetle species encounter the landscape while foraging and reproducing. Within such an area, fragmentation may favor predator functional diversity. Forest gaps that contain woody debris can harbor a greater abundance of cerambycid and clerid species than surrounding edge and forest habitats (Ulyshen et al., 2004). In these gaps, resource availability and quality may have been increased for the wood-borers, attracting a greater number of them. This in turn may have promoted an increase in the clerid predators. In my study, fragmentation at this focus may harbor greater abundance of both wood-borer and predator species similar to findings of Ulyshen et al. (2004), but perhaps the predator species found in these sites had more diverse trait profiles resulting in an increase of FRic of this group. The exploration of this pattern may be done with further investigation of species diversity versus functional diversity in future studies.

While constructing these 3D curves, I could not select *a priori* which landscape metrics measured at a particular focus would best describe the relationship between all functional diversity indices of wood-borers and their predators. Furthermore, at the functional group level I could not investigate changes in FEve, FDiv, and FRic because

some sites along the gradient contained too few species per functional group to calculate these indices. But, 3D surfaces of the other FD indices (FDis, FDiv, and FEve) may provide further insight on how functional diversity changes with habitat disturbance. Considering that these may not be restrictions in future studies, 3D surfaces of these indices (FRic, FEve and FDiv) at the functional group and community levels may complement analyses such as multiple regression to study changes in functional diversity. However, FD index values may vary considerably within communities. For example, in my work trait space volumes (FRic) between wood-borer and predator communities differed by several orders of magnitude. Meaningful comparisons therefore may require scaling of the different groups.

3.4.1 Conclusions

I demonstrated that response to the landscape, even at the functional diversity level, varies with focus. I proposed that assessing functional diversity at ecologically relevant foci is important for capturing its response to habitat change. Following this approach, management to conserve functional diversity may be possible for local landscapes. The methods I presented here that outline how to produce 3D curves of functional diversity at a community level may be incorporated into a possible strategy given that information is available on the functional role of species of interest. These curves could be used to select appropriate landscapes for maximizing functional diversity based on surrounding landscapes. However, the construction of these curves should involve: 1) standardization of functional diversity indices and 2) assessment of functional diversity response across foci. Considering that functional diversity is assessed with the

same explanatory variables, curves may then be plotted together, and the resulting plot would simultaneously reveal which landscapes are most appropriate for maximizing functional diversity of multiple communities, or even those that favor ecosystem service providers over pestiferous groups.

These methods have broad management applications. Ecological trends from the 3D curves along the landscape gradient could be distilled into maps that categorize the landscape based on how appropriate they are for various management goals. For instance, these maps could target sites that would be appropriate to place tree stands, orchards, or landscapes that would maximize forest health. Overall, the maps that would be dissiminated to land managers would indicate, based on color, how appropriate locations are for the management goal.

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CHAPTER 4: DETECTION OF ECOLOGICAL STABILITY MECHANISMS ACROSS TROPHIC LEVELS

4.1 Introduction

Human activity is the leading cause of current changes to biodiversity (Sala et al. 2000), and increasing habitat fragmentation and loss are primary contributing factors to this decline (Brook et al. 2003, Pereira et al. 2010, Rands et al. 2010). Such disturbances alter biodiversity resulting in a negative impact on ecosystem function (Hooper, et al. 2005, Tilman et al. 2014) including processes like pollination, nutrient cycling and seed dispersal. There has been growing interest in understanding diversity's role in the mechanisms behind ecosystem resilience (Folke et al. 2004) with much attention focusing on how functional diversity, or variation in species' ecological roles, impact ecosystem function (Tilman et al. 1997, Díaz & Cabido 2001, Heemsbergen et al. 2004, Dang et al. 2005, Scherer-Lorenzen 2008). The functional insurance hypothesis states that stability in ecosystems is maintained by species that perform similar functions but have asynchronous responses to disturbance (Johnson et al. 1996, Yachi & Loreau 1999). According to the functional insurance hypothesis, an increased number of species with similar ecological function buffers communities from environmental change. If there are many species performing a similar role and one is lost from the community, the persistence of the other species allows for the function to continue. The functional insurance hypothesis has been supported by theoretical modeling that found that species

richness enhanced ecosystem productivity and the variation in species responses (Yachi & Loreau 1999). In controlled experiments, the functional insurance hypothesis was supported in microbial microcosms (Naeem & Li 1997, Leary & Petchy 2009), and among birds in coffee agroforestry systems (Perfecto et al. 2004).

There are three proposed stability mechanisms that are related to the functional insurance hypothesis including cross-scale resilience, response diversity, and density compensation; all of which involve asynchronous species' response to environmental change (Figure 4.1). I investigate each of these in the work described here. Cross-scale resilience occurs when species' asynchronous responses occur at different foci (Fig. 4.1A). If cross-scale resilience is operating within a community, species with similar ecological function respond to disturbance at different analytical foci (Peterson et al. 1998, Steffan-Dewenter et al. 2002). Here, I refer to the analytical focus as the size to which study grain is aggregated into replicates (sensu Holland & Yang in press) as the analytical focus (hereafter called "focus"). The focus can be visualized by the radius around a point at which surrounding landscape features are assessed. With respect to cross-scale resilience, some species may respond to changes in the landscape at a local-level focus, thus being unaffected by more distant disturbances while for other species the opposite is true. Ecosystem stability is achieved when this asynchronous response to disturbance is distributed among species having similar functional roles. Cross-scale resilience is indicated if an environmental change impacts species' abundances at different foci when these species share an ecosystem function. Winfree and Kremen (2009) used the most explanatory focus for each species as evidence of cross-scale resilience. Generally the most explanatory focus of a species is determined by

investigating the relationship between the abundance of the species of interest and landscape assessed among a range of foci then selecting the focus with the best explanatory power for the relationship between species and landscape (e.g., Holland et al. 2004). However, I present new methodology that considers the overall trend of species' response to changes in landscape pattern measured across all relevant foci. I group species based on the similarity of these trends and examined how ecosystem function was distributed within different landscape response trends. Cross-scale resilience would be supported where species with similar functional roles have different responses to the same environmental change across foci.

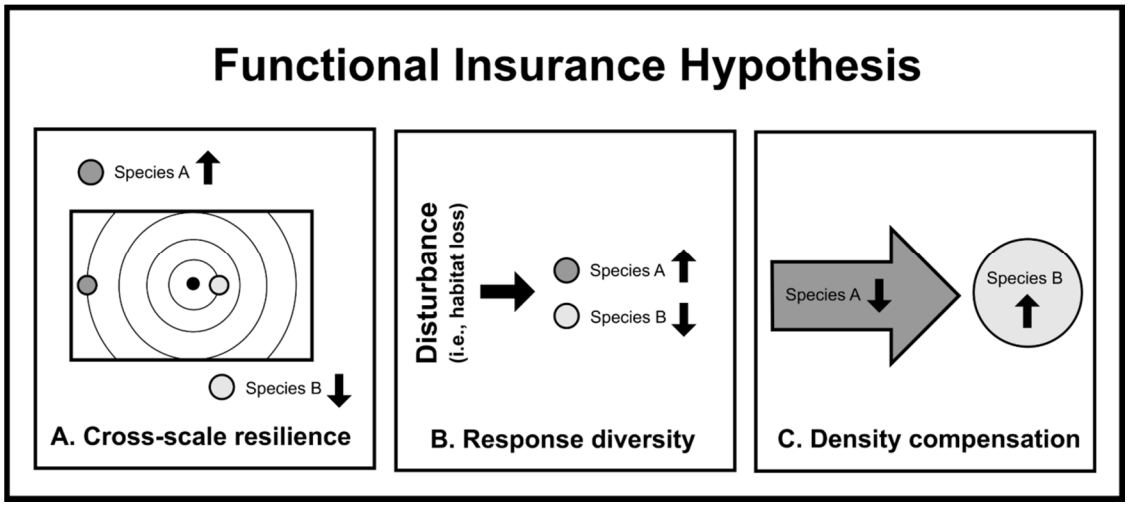


Figure 4.1. Three proposed stability mechanisms related to the functional insurance hypothesis. These mechanisms provide ecosystem resilience through the asynchronous responses of species with similar ecological function.

Response diversity is a second proposed stability mechanism that also results from asynchronous response of species to environmental change. If response diversity is occurring in a community, an environmental change causes populations of some species to increase while causing populations of other species to decrease (Chapin III et al. 1997,

Walker et al. 1999, Elmqvist et al. 2003, Nyström 2006, Chillo et al. 2011) (Fig. 4.1B). If this asynchronous response to environmental change occurs among species with similar functional roles, ecosystem function is stabilized. In this study, I consider response diversity present if there is asynchronous response to environmental change among species within functional groups.

Density compensation is a third possible mechanism through which diversity stabilizes ecosystems where the asynchronous response results from the decrease in abundance of one species being followed by an increase in the abundance of another species (Naeem & Li 1997) (Fig. 4.1C). Density compensation may result from interspecific competition, in particular competitive release (Tilman 1999). Considering species with similar ecological roles, a dominant species may respond negatively to disturbance, which in turn allows competing species to increase in abundance. If density compensation is operating among species with similar ecological roles, the function will not be lost within the community.

Evidence for these proposed mechanisms of functional stability has been found in diverse systems. For instance, cross-scale resilience was detected in a study examining bee pollinator response to a gradient of natural vegetation around watermelon farms (Winfree & Kremen 2009). Response diversity was discovered in *Arabidopsis thaliana* where *A. thaliana* ecotype metabolite responses and biosynthetic pathways and processes differed under ambient and elevated CO_2 conditions which influenced the plants' phenotypic expression of growth and development (Li et al. 2006). Density compensation was found in aquatic microcosms (McGrady-Steed & Morin 2000) and ant species assemblages along an elevation gradient (Longino & Colwell 2011).

Here I use specific tests, including new methodology to test for cross scale resilience, to determine which of the above types of asynchronous response are contributing to stability of a predator and prey community. The presence of these mechanisms in the system supports the functional insurance hypothesis. Specifically, I investigate the presence of cross-scale resilience, response diversity, and density compensation in a multi-trophic system consisting of longhorned beetles (Coleoptera: Cerambycidae) and their generalist beetle predators (Coloeptera: Cleridae, Cucujidae, Histeridae, Passandridae). I have previously grouped these beetles into functional groups based on their diverse ecological roles in hardwood forests as larvae and as adults (Chapter 3). In this study I use these functional groupings and the variability of how species abundance within these groups changes along a gradient of habitat fragmentation to detect the presence of these three proposed ecological stabilizing mechanisms and find support for the functional insurance hypothesis.

I expect to detect all three stabilizing mechanisms and thus support for the functional insurance hypothesis in this system. Specific to cross-scale resilience, I previously found that these predator and prey species have different landscape response trends (Chapter 3) and that the longhorned beetle species included in the study responded at different foci (Yang 2010). The longhorned beetles may be responding to many local (e.g., moisture, vertebrate predators, dead-wood availability) and landscape factors [habitat fragmentation, density of habitat edges, variation in habitat quality (Abdel Moniem & Holland 2013)]. The predators would also be influenced by local and landscape factors. Here I have developed methodology to identify how species respond to the landscape across foci and apply this approach to detect cross-scale resilience which

would be indicated by different response trends across all foci important for the species. In this study the presence of response diversity would be indicated by species within functional groups responding differently to the same disturbance. Previous studies on the wood-borer and generalist predator systems are sparse and none include more than a few species in the study. But, Costa et al. (2013) demonstrated that two predator beetle species, a clerid and a histerid, were affected differently by habitat fragmentation. I have also found that predator and longhorned beetle functional groups respond differently to fragmentation (Chapter 3). Specifically, I measured change by two measures: 1) functional redundancy, the number of species within functional groups, and 2) functional dispersion, the within-functional group dispersion in trait space, a measure that incorporates species abundance and its distribution within functional trait space. I found that both functional redundancy and functional dispersion was altered by forest fragmentation. This indicates that the species within my functional groups have dissimilar responses to disturbance. Interspecific competition has been proposed as a mechanism underlining density compensation where the increase in the abundance of one species results in the decrease in abundance of another species (Tilman 1999). Although I do not have data on which species are dominant competitors, I would expect that interspecific competition is likely within functional groups because of their similar resource utilization. For instance, beetles within the same functional group are more likely to occur in the same habitats and compete for similar host resources based on having similar ecological niches. Following this logic, I also expect to find density compensation operating in this system, indicated by species increasing in abundance while others decrease in abundance.

4.2 Methods

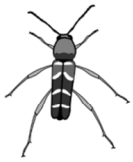
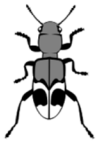
4.2.1 Beetle sampling and functional groups

I used abundance data of longhorned beetles and their generalist beetle predators within sites sampled in three projects, the Upper Wabash Ecosystem Project (UWEP) (Swihart et al. 2006), the Hardwood Ecosystem Experiment (HEE) (Saunders & Swihart 2013), and an across-state beetle survey (Holland 2006) in Indiana, USA. Sites within these projects were selected to represent a forest fragmentation gradient. The forest habitat was secondary growth forest fragmented by agricultural and urban land use. The range of the fragmentation gradient measured at a 2 km radius was from 100% to approximately 5% forest. At each site, beetles were trapped in an array of traps consisting of one Lindgren multiple funnel trap (12 funnel size; Phero Tech, Delta, Canada), one Intercept panel trap for bark beetles (Integrated Pest Management Tech, Portland, OR), and one multi-pane window trap, all baited with 99% ethanol (Holland 2006). Trapping lasted 70 – 90 d over the summer of 2006 (UWEP) and 2007 (HEE). Longhorned beetles were identified to species using Yanega (1996), Linsley (1962a, b, 1963, 1964), Linsley & Chemsak (1972, 1976), Arnett et al. (2002a, b) and Downie & Arnett (1996a, b) while I identified all predator species in the families Cleridae, Cucujidae, Histeridae, and Passandridae to species using keys in Arnett et al. (2002a, b, Downie & Arnett 1996a, b). All specimens reside in the Landscape Ecology & Biodiversity laboratory at Purdue University.

I grouped beetle species into functional groups based their ecological roles in hardwood forests (Table 4.1). Table 4.1 contains information on the principal traits that differentiate the functional groups and the number of longhorned beetle and predator species each contain. The same species do not appear in multiple functional groups. Many functional traits were

acquired from literature sources. I also calculated a novel functional trait, landscape scale response, for each species, to take into consideration how a species responds to changes in the landscape. I compiled an additional novel trait, avian visual perception of beetles, which considers the inter-trophic interaction between insectivore birds and their beetle prey. Further information on how these functional groups were obtained is outlined in Chapter 3.

Table 4.1: Longhorned beetle and predator functional groups, the major traits that discriminate them, and the number of species they contain. Species are only found in a single functional group.

	Functional Group	Discriminating Traits	# Species/ Functional Group
Longhorned beetles 	**FG1**	nocturnal/crepuscular larvae attack branches and twigs feeds on hardwoods, shrubs, vines, herbs	28
	FG2	adult flower feeding linear landscape response trend	8
	FG3	larvae feed on all parts of dead hardwoods	45
Predators 	**FGA**	feeds on eggs and larvae found in dead hardwoods avian visual perception category 1	13
	FGB	feeds on all life stages found on living and dead hardwoods and conifers	11

4.2.2 Landscape assessment

I selected the proportion of forest cover across the landscape to assess habitat loss and create a gradient of sites differing in habitat loss. Proportion forest was measured at twelve foci spanning radii of 0.03 – 7.29 km around field sites with a binary map of forest cover/non-forest cover using GRASS GIS (GRASS Development Team, 2012). Specifically,

the twelve focus radii were 0.09 km, 0.15 km, 0.27 km, 0.45 km, 0.63 km, 0.81 km, 1.35 km, 1.89 km, 2.43 km, 4.05 km, 5.67 km, and 7.29 km (Appendix C, Table C.1).

4.2.3 Ecosystem stability mechanisms

4.2.3.1 Cross-scale resilience (Fig. 4.2, I)

I wished to characterize species' landscape response by considering the entire trend (explanatory power vs. landscape focus) across all relevant foci. This produced landscape response trends for each species, after which I grouped species based on the similarity of these trends. In this study, cross-scale resilience would be present if species within each functional group were equally distributed within different landscape response trends (e.g., species with similar functional roles respond to the same environmental change differently across foci).

The beetle data were count data that did not meet linear assumptions. Therefore I calculated Spearman's rank correlation coefficients (Spearman 1904) (rho) for the abundance of each beetle species with the proportion of landscape at each of the twelve foci. I performed Ward's clustering (Legendre & Legendre 1998, p. 329 – 333) on the Euclidean distance of a matrix containing |rho| values at each of the twelve foci for each species. I then used scree plots to determine the appropriate pruning height to obtain groups of species' landscape response trends. I used loess smoothing of curves (Cleveland 1993, p. 93–101) within trend groups to visualize the landscape response trends. I constructed a contingency table of the number of species within each functional group across landscape response trends and statistically tested for independence with a Chi-square test (Meng & Chapman 1966). An insignificant Chi-square test would indicate that species within functional groups are

similarly distributed across response trends, therefore species within a given functional group respond differently to the same environmental disturbance across the range of ecologically relevant foci. Thus, there would be more resilience to disturbance within these groups. All analyses were performed using R (R Core Team 2014).

4.2.3.2 Response diversity (Fig. 4.2, II)

My test for the presence of cross-scale resilience included the entire trend of species' response to landscape pattern. However, I wished to determine the single best explanatory focus of each of the beetle species to use in the test for the presence of response diversity within functional groups. Approximately 21% of the beetle data were overdispersed (the variance exceeded the mean) using Poisson general linear models (AER package, R (Kleiber & Zeileis 2008)). Therefore I followed a quasi-Poisson generalized linear model framework which is less restrictive for overdispersed data (Ver Hoef & Boveng 2007). I constructed quasi-Poisson generalized linear models at each focus where beetle abundance was a continuous response variable and proportion landscape was a continuous predictor variable. I obtained the |t-value | from these models and selected the focus with the highest |t-value| as the most explanatory focus in the statistical models (below).

Response diversity occurs when species respond differently to a disturbance event. I tested for the presence of response diversity by constructing another set of quasi-Poisson general linear models. Beetle abundance within functional groups was a continuous response variable, beetle species within functional groups was a categorical predictor variable, and proportion landscape at the most explanatory focus for each beetle species (calculated above) was the continuous predictor variable. I used the interaction term between beetle species and habitat loss to determine if the population response to habitat amount varied among the

different beetle species within a functional group (Winfree & Kremen 2009). Thus, the significance of this interaction term in the quasi-Poisson generalized linear model was used to test for the presence of response diversity within functional groups. All analyses were performed in R (R Core Team 2014).

4.2.3.3 Density compensation (Fig. 4.2, III)

Density compensation occurs when the decrease in abundance of one species is followed by an increase in the abundance of another species that contributes to the same ecosystem service (Winfree & Kremen 2009). I considered species within the same functional group as contributing to the same ecosystem processes based on their similar ecological roles. Within functional groups I assessed all pair-wise species covariances across the sites along the deforestation gradient (Pearson's *r*). I transformed species within each functional group by calculating the natural log of (species abundances + 1). Using transformed species abundances, I calculated all pair-wise species covariances. I plotted a frequency distribution of these to examine for the presence of density compensation (Winfree & Kremen 2009). A frequency distribution shifted to the left of zero would suggest density compensation (Winfree & Kremen 2009). I statistically tested whether these distributions are shifted to the left of zero. The variance ratio test was introduced by Schluter (1984) to test the statistical significance of the covariances of species' abundances. However, the variance ratio test utilizes presence/absence data, not raw species abundance, so was inappropriate for my study. Since frequency distributions of Pearson's *r* were not normal, I used one-sided Wilcoxon signed rank tests (Taheri & Hesamian 2013) to test whether the median pair-wise species covariance was less than zero. All analyses were performed in R (R Core Team 2014).

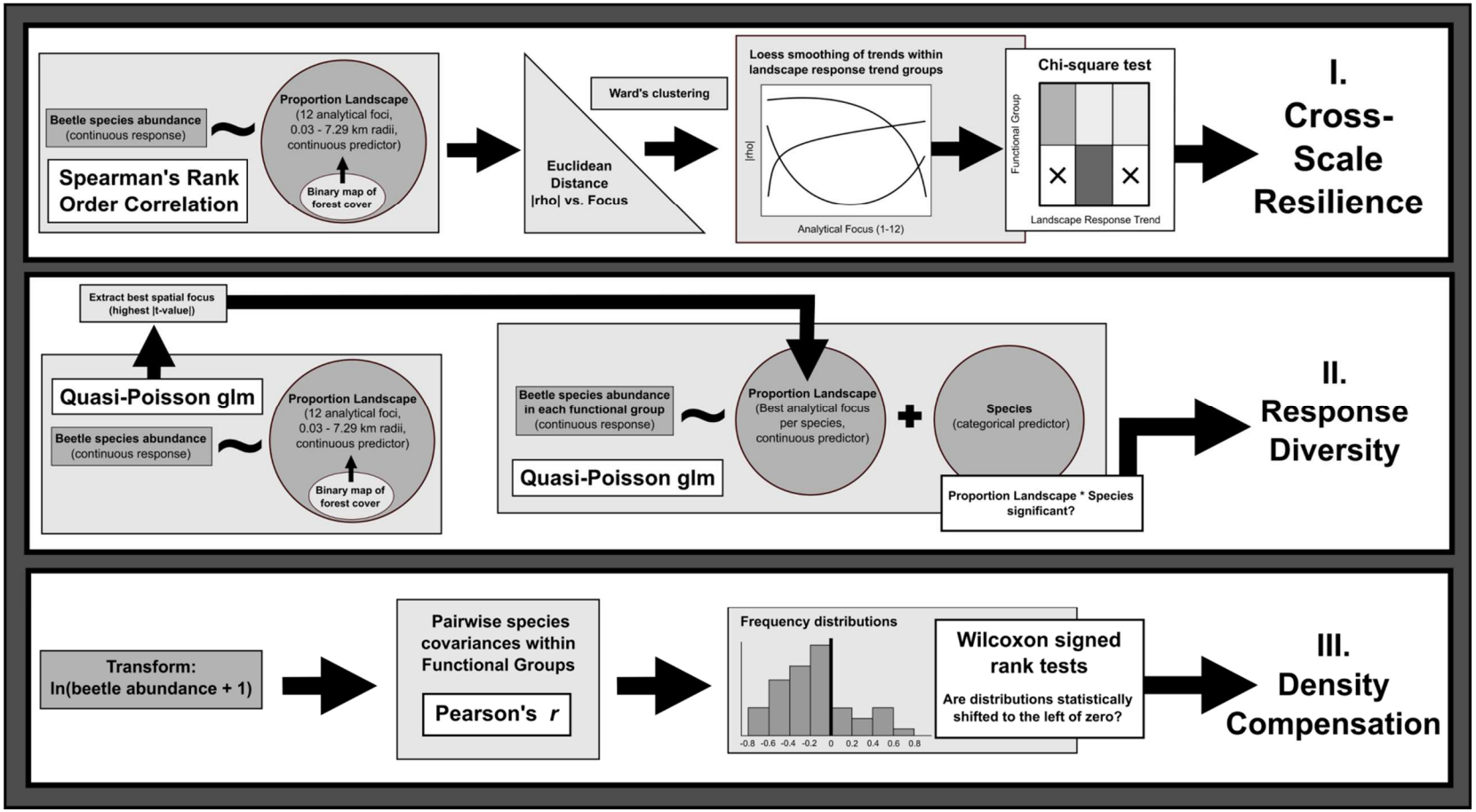


Figure 4.2. Flowchart depicting methods used to detect the three proposed stability mechanisms: cross-scale resilience, response diversity, and density compensation.

4.3 Results

I found evidence that cross-scale resilience and response diversity but not density compensation, were operating within predator and wood-borer functional groups. Among predator and longhorned beetle species there were six landscape response trends (Figure 4.3). Most landscape response trends were parabolic, but Trend 1 continued to increase within the foci selected for the study.

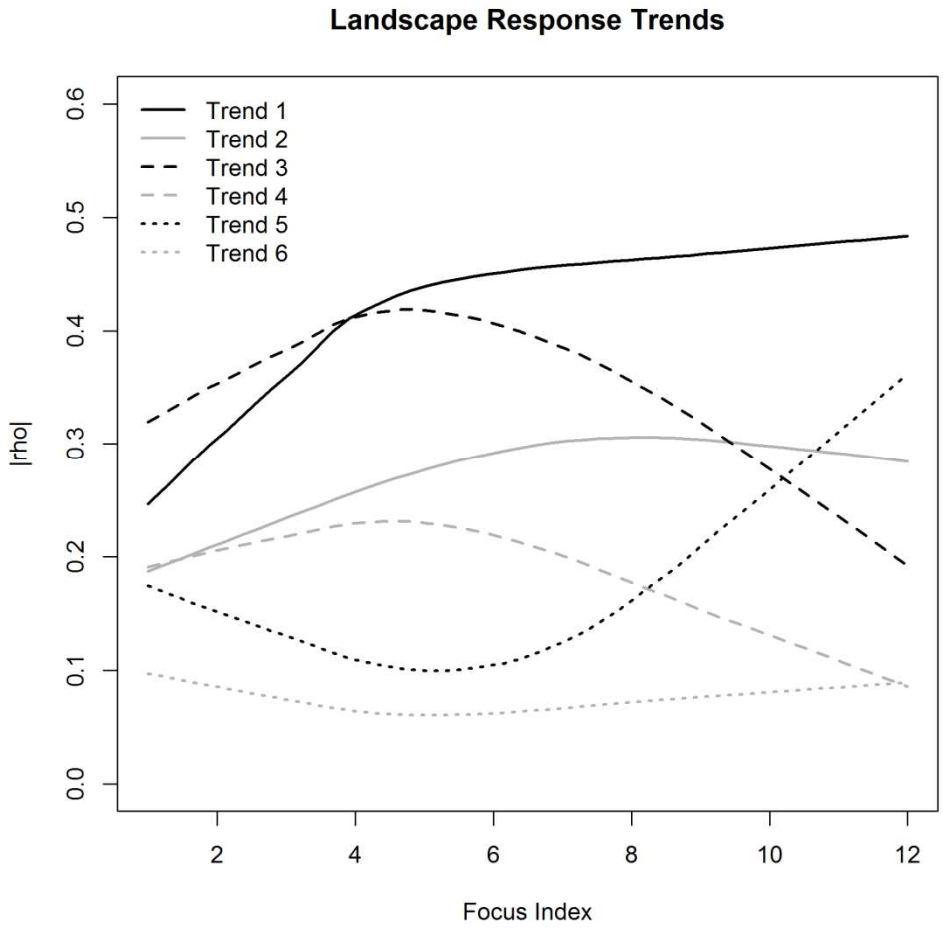


Figure 4.3: Six landscape response trends generated from loess smoothing of |rho| vs. analytical focus of each beetle species grouped by Ward's clustering.

I found that the Chi-square test of the contingency table of number of species within each functional group across landscape response trends was not significant (χ^2 = 26.69, df = 20, p = 0.14) (Table 4.2). Therefore, species within each functional group were distributed similarly across the different landscape response trends (Table 4.2).

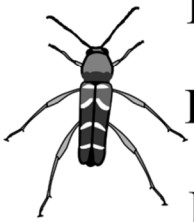
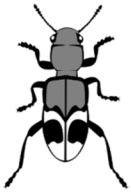
Table 4.2: Contingency table containing the number of species within each functional group that have the same landscape response trend

		Landscape Response Trend						
		Trend 1	Trend 2	Trend 3	Trend 4	Trend 5	Trend 6	Total
Functional Group	FG1	3	2	2	10	3	8	28
Longhorned beetles	FG2	0	4	0	2	0	2	8
	FG3	3	8	4	8	8	14	45
Predators	FGA	1	0	4	4	1	3	13
	FGB	0	3	0	3	3	2	11

χ^2 = 26.69, df = 20, p = 0.14

Response diversity within each functional group was assessed with the significance of the species-proportion landscape interaction term in a quasi-Poisson generalized linear model. The response variable was the abundance of beetles within each functional group. The interaction term in the generalized linear model was significant for all functional groups except “FG2” (Table 4.3), giving support for the presence of response diversity in these groups.

Table 4.3: Significance of the interaction terms from the quasi-Poisson generalized linear models indicating the presence of response diversity within each beetle functional group.

	Functional group	Coefficient	*t*-value	*p*-value
Proportion landscape : Species	 **FG1**	0.16	5.48	6.03e-08
	FG2	0.30	1.19	0.24
	FG3	-0.18	-7.36	3.49e-13
	 **FGA**	-0.50	-5.45	1.03e-07
	FGB	-0.26	-2.15	0.03

*Model calculated using the most explanatory focus for each species in each functional group

Visualization of the frequency distributions of Pearson's *r* did indicate that abundance of longhorned beetle functional groups, "FG2" and "FG3" had some shift below zero (Fig. 4.4: B, C). However, I found no statistical support for any functional group having density compensation. All Wilcoxon signed rank tests were not significant (given in Figure 4.4) indicating that the median pair-wise species covariance for each functional group was not less than zero.

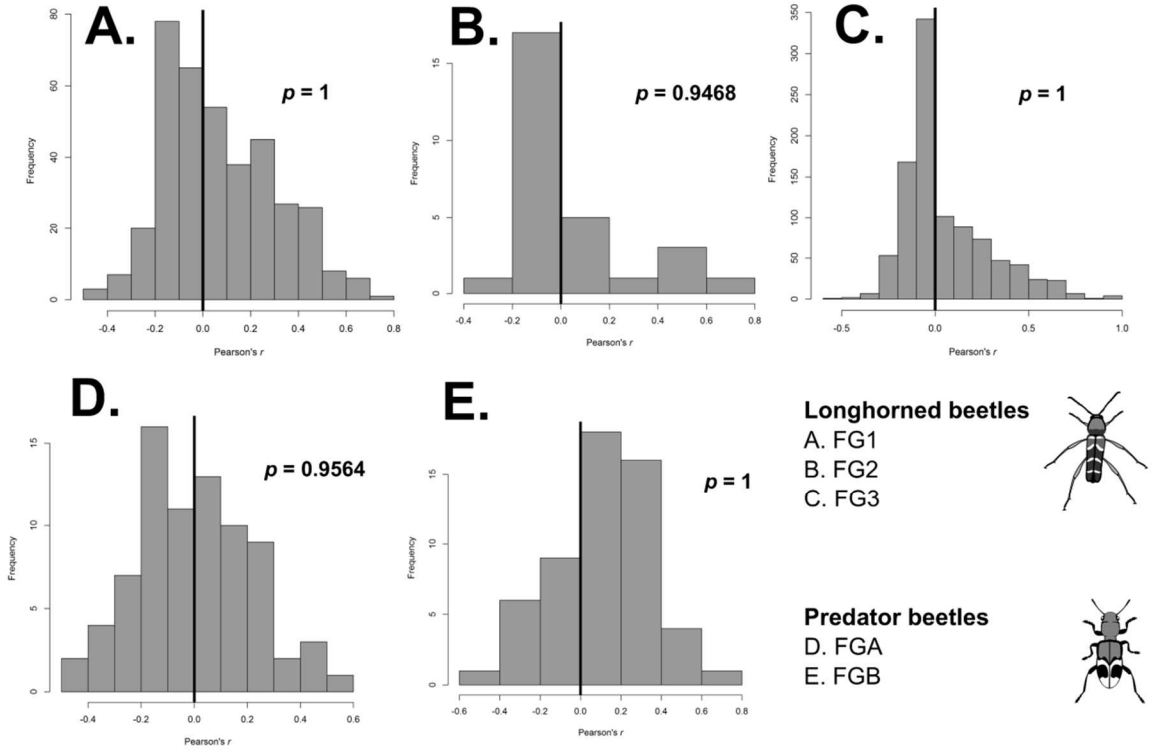


Figure 4.4. Frequency distributions of Pearson's *r* to visualize presence of density compensation (negative covariance between species) within each functional group. Whether there were more negative than positive correlations between species within each functional group was tested with Wilcoxon signed rank tests (*p*-values are given in bold).

4.4 Discussion

I tested new methodology to detect cross-scale resilience within communities across a landscape assessed at multiple foci. This approach was successful because it 1) considered all species' responses across species-relevant foci, 2) grouped species based on similar landscape response trends, and 3) considered whether ecosystem function was similarly distributed among these trends. Overall, this provided an ecologically relevant test for this stability mechanism because it determined how species respond across the entire landscape relevant to their ecology (i.e. dispersal and foraging behavior), and not

just at a single landscape focus. Furthermore, grouping species based on these response trends and examining how ecosystem function is distributed among species within these groups enabled us to test for the operation of this mechanism.

I found support for cross-scale resilience and response diversity in the community of predator and prey functional groups. Species' response to the landscape followed different, distinct foci response trends and, more importantly, my approach to detect cross-scale resilience revealed that species within functional groups were similarly distributed among these trends supporting the presence of cross-scale resilience in this community. I also found support for response diversity in the system within four out of five functional groups. Specifically, the significant interaction term of the quasi-Poisson models indicated that species within these four functional groups responded differently to forest loss. Both the diversity of functional roles and the diversity of responses to environmental change by species that have similar ecological function are important for maintaining ecosystem stability (Walker 1992, Elmqvist et al. 2003). "FG2" was the functional group within which response diversity was not detected. This group contained the fewest species making it less likely that I could detect differing responses to disturbance.

I did not find support for density compensation within any functional group in the system. Density compensation would have been indicated by a shift in the frequency of pair-wise species correlations (Pearson's *r*) to the left of zero. Interspecific competition was proposed by Tilman (1999) as a mechanism underlining density compensation. Under this premise, as a dominant species becomes less abundant along a disturbance gradient, less-dominant species increases in abundance through competitive release. I do

not know which species are dominant in the system thus am not able to determine whether interspecific competition was actually operating in the system. But, I found that there were more positive than negative correlations between species (Figure 4.4). Species can respond positively to climate events such as El Niño where for example increased rainfall heightens plant productivity causing a bottom-up effect on herbivores and carnivores (Holmgren et al. 2001). Furthermore, species tend to increase in abundance in environments with favorable resources. For instance, it was found that the abundance of Cerambycidae regardless of functional role increased with declining hardwood tree productivity (Raje et al. 2012). Forests with declining productivity may contain more deadwood and stressed trees which provide more favorable conditions for longhorned beetles (Raje et al. 2012). Also, wood-borers and their beetle predators can have similar attraction to semiochemicals and other stimuli from their host trees (Reddy & Guerrero 2004) and with respect to the predators to their prey (Pajares et al. 2004). These responses to semiochemicals could potentially result in positive correlations among these species.

I predicted support for density compensation because species within the functional groups performed similar ecological roles in similar habitats. If resources are limited, interspecific competition is likely under these conditions. Therefore, as dominant species became less abundant along the fragmentation gradient, species repressed from dominant competitors would increase in abundance (Tansley & Adamson 1925). However, this may not be the case if species with similar ecological function respond to the landscape at different foci. It is known that species respond to the landscape at different foci (Addicott 1987), and I found support for cross-scale resilience

in this study. Cross-scale resilience would be operating if, among species with similar function, species responding at local foci are not affected by distant disturbance and species responding at large foci are not affected by local disturbance. This differing response to landscape pattern by species with similar ecological function works to stabilize communities from disturbance. Interactions among species that respond at the same focus may be greater than the interactions among species that respond at different foci (Peterson et al. 1998). Peterson et al. (1998) hypothesized that if species within functional groups respond to changes in the landscape at different foci, competition among them would be reduced while still fortifying ecosystem function. Thus, species with similar function that respond to disturbance in the landscape at either local or regional foci enable ecosystem processes to persist. In this study, species within functional groups responded to the landscape at different foci which would theoretically buffer ecosystem function from disturbance whether occurring at a local or a landscape level. This potentially would also reduce interactions among species (including competitive interactions between them), causing the lack of detection of density compensation in this system.

Similar to my study, cross-scale resilience (and not density compensation) was detected in wild bee communities in watermelon farms (Winfree & Kremen 2009). The authors attributed the lack of detection of density compensation to fewer resources for species in landscapes with less native vegetation along environmental gradients. Therefore, species that would normally benefit from competitive release did not increase in abundance due to poor resource availability. Cross-scale resilience may stabilize ecosystem function through species' variable tolerances to disturbance. Increased

isolation of habitat patches decreases the probability that a given species is able to cross unsuitable habitat to reach necessary resources. Under this premise, some species' superior dispersal ability allows them to persist across the landscape at a regional level while being extirpated at a local level (Huffaker 1958).

Determining further mechanisms underlining cross-scale resilience is beyond the scope of this study. However, future directions could examine species' variable dispersal abilities through mark and recapture experiments and modeling of net displacement (Cushman et al. 2013) or diffusion modeling (Cronin et al. 2000) to give further insight into whether the detection of cross-scale resilience in this study could be due to the variation in the dispersal ability of the species. Species in this study demonstrated different trends to changes in the landscape. Therefore, within functional groups it is likely that some species are better dispersers than others. It has been demonstrated that predator beetle and prey wood-borer beetles differ in dispersal ability and edge behavior. The predator beetle in the family Cleridae, *Thanasimus dubius*, is known to disperse farther than its prey (Costa et al. 2013). Furthermore, this species is restricted to pine forest whereas the prey could disperse into open areas outside of pine forest (Costa et al. 2013). Although such trends for the predator beetles in my dataset are unknown, similar phenomena may be operating in this system of woodborers and predator beetles. However, specific dispersal distances of all species in my dataset have not been quantified.

To my knowledge no previous work has aimed to detect these three stabilizing mechanisms (density compensation, response diversity, and cross-scale resilience) within a multitrophic system with already established functional groups of predator and prey

species. I propose that there was a lack of evidence for density compensation operating in this community because species within functional groups responded to changes in the landscape differently which reduced species interactions within functional groups. Under this premise, interspecific competition would have been reduced between species, weakening the signal of density compensation. Systems with high resource availability may also reduce competition thus prevent competitive release (Wiens 1977). However, there was no resource pulse in my system (e.g., no plentiful deadwood resources resulting from recently cut forest). I did find asynchronous responses to disturbance among species within the same functional group and also across landscape response trends giving support that cross-scale resilience and response diversity were operating in this community. Furthermore, considering that these mechanisms were not only present within functional groups but also at both trophic levels, these results suggest that there was a persistence of ecosystem function within this community despite loss of habitat.

Although not considered in this study, there are several other proposed stability mechanisms. The portfolio effect is based on the economic principal that more diverse portfolios are more stable (Lee et al. 2009, p. 249) and achieved through the effects of statistical averaging. The important feature of the portfolio effect in ecology is that more diverse communities are more stable (Tilman et al. 1998, Tilman 1999). Niche complementarity stabilizes ecosystems through the complementary use of resources in an ecosystem by functionally distinct species or groups of species (Kahmen et al. 2006). However, if a functional group disappears from the ecosystem, its niche becomes vacant and the ecosystem function resulting from their unique utilization of resources is lost (Kahmen et al. 2006). Facilitation is "an interaction in which the presence of one species

alters the environment in a way that enhances growth, survival, and reproduction of a second species" (Bronstein 2009). A facilitating species contributes to ecosystem stability by increasing species diversity of the species that are favored by the altered environment which can lead to increased trait dispersion in local communities (reviewed in McIntire & Fahardo 2013).

Effort to maintain ecosystems should promote functional richness and high redundancy of species within functional groups. Effort could be planned in managed systems at a local scale by considering surrounding conditions at the larger scale. For instance, I previously established beetle functional groups and developed methods consisting of three dimensional (herafter, 3D) curves that indicate the degree of fragmentation measured at the most explanatory focus that best promotes beetle community functional richness (Chapter 3). This 3D curve approach could be used to determine the level of management that best promotes functional richness and high redundancy among these taxa. For instance, the 3D curves could be used to determine appropriate landscapes for placing tree stands destined for timber harvest and orchards. Also, they could be used in management that promotes local forest health. Future work should aim at determining the level to which these stabilizing mechanisms buffer ecosystem processes from disturbance in controlled experiments. Identifying the stabilizing mechanisms in operation in addition to a quantified result of an ecosystem process would also provide pertinent knowledge to preserve ecosystem function.

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CHAPTER 5: CHANGES IN COMMUNITY STRUCTURE ARE LINKED TO VISION-MEDIATED PREDATOR-PREY INTERACTIONS

5.1 Introduction

The interplay between predator and prey can affect population dynamics (Zvereva & Kozlov 2006) and ultimately ecosystems (reviewed in Pace et al. 1999). Within hardwood forests, wood-boring beetles are prey to both predacious beetles and insectivore birds. The wood-borers are important insects in these systems by serving as nutrient cyclers (Gutowski 1987, Edmonds & Eglitis 1989), pollinators (Linsley 1961, Kevan & Baker 1983), or can be significant pests of living trees (Shibata 1987). Their beetle predators feed on all life stages of wood-borers thus also play a role in forest health (Böving & Champlain 1920). Furthermore, insectivore birds are significant predators of beetles, depredating abundant insect prey (The Birds of North America N.D.). Habitat fragmentation impacts the diversity of these beetles' functional roles (Chapter 3) and populations of forest insectivore birds (Chalfoun et al. 2002). However, it is also important to consider the predator-prey interactions between these three trophic levels to have a better grasp on the overall functioning of hardwood forest ecosystems.

The behavioral ecology of predator-prey interactions has received much attention particularly in relation to vision-mediated behavior of birds (i.e., Kettlewell 1955, Stuart-Fox et al. 2003, Zampiga et al. 2006, Stoddard & Stevens 2011). These studies have yielded interesting and important insights into the complexity of vision-mediated

predator-prey interactions. However, to my knowledge, no previous study has examined how vision-mediated behavior of an avian predator impacts species abundances across trophic levels at the community level. Here, I describe new methods to link predator and prey trophic levels to examine how the visual system of avian predators and the appearance of their beetle prey impact the structure of this community. Importantly, these methods are transferable across all taxa depending on available knowledge of the visual system of the predator and the ability to directly measure prey reflectance and irradiance of relevant environmental light conditions.

Many animals use crypsis or aposematic warning patterns (Stevens 2007) as a defense against predation. Under the strategy of Batesian mimicry, non-harmful species resemble harmful species in appearance and behavior (Ohsaki 1995). However, the success of these strategies depends on how visually apparent such patterns are to potential predators. Years of research on the anatomy and physiology of vertebrate and invertebrate eyes, particularly in the past several decades, have demonstrated that diverse visual systems exist among animals (i.e. Walls 1942, Briscoe & Chittka 2001, Bowmaker 2008, Skorupski & Chittka 2010). Birds, for example, have extraordinary color vision that surpasses the visual capabilities of a human (reviewed in Chapter 2). One major distinction between human and avian vision is that many birds are able to discriminate colors extending into UV wavelengths, to which humans are blind. Both birds and humans have the ability to distinguish reflectance in long-wavelengths, so it is possible that they share some common visual perception of warning coloration (Lindstedt et al. 2011). But, differences in the UV component of aposematic patterns between the mimic and the model may exist (Remington 1973), and what may appear to have cryptic

coloration to a human may actually be visually apparent to a bird (Church et al. 1998). Therefore we need to take a "bird's eye view" of prey if we want an ecologically relevant picture of avian vision-mediated predator-prey interactions.

The most direct approach that has been developed so far consists of using models that incorporate spectroradiometric measurements and vision physiology of the organism of interest. One such model proposed by Vorobyev et al (1998) measures 1) the reflectance of two objects, 2) the irradiance of ambient light conditions under which the objects are viewed, and obtains 3) the physiological properties of the viewer's visual system. The two objects are ordinated within the vision space according to the relative stimulation of the viewer's photoreceptors, and the Euclidean distance between the two objects is calculated. This distance represents the visual contrast between the two objects, and if the distance value falls past a given threshold, these objects are theoretically discriminated by the viewer (Vorobyev & Osario 1998). Considering that birds are tetrachromats, the vision space occupied by birds consists of a three-dimensional tetrahedron. The axes of the tetrahedron consist of the spectral sensitivities of the photopigments in each of their four single cones: SWS1 (which is UV- or violet sensitive), SWS2 (blue-sensitive), RH2 (green-sensitive), and LWS (blue-sensitive) (Figure 5.1). A review of bird vision is given in Chapter 2.

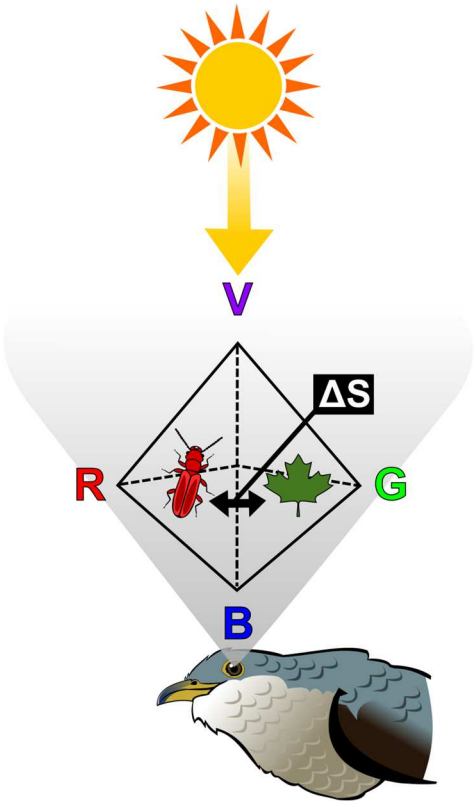

Figure 5.1: Hypothetical depiction of the visual contrast between *Cucujus clavipes*, a predator beetle, and a maple leaf, *Acer saccharum*, under full sunlight within avian tetrahedral color space of the yellow-billed cuckoo, *Coccyzus americanus*. V = violet-sensitive photoreceptor; R = red-sensitive photoreceptor; G = green-sensitive photoreceptor; B = blue-sensitive photoreceptor; ΔS = chromatic contrast.

Bird vision models have been used, for example, to examine the visual discrimination of bird plumage patterns (Benites et al. 2010) and eggs of nest parasites from the eggs of the host species (Stoddard & Stevens 2011). They have also been used to investigate how vision mediates fruit discrimination (Schaefer et al. 2006, Schaefer et al. 2007, Fadzly et al. 2013) and predator-prey interactions (Maan & Cummings 2012). Specific to predator-prey interactions, the appearance of prey according to their avian predators has been studied in a wide range of taxa including poison dart frogs (Siddiqi et al. 2004, Maan & Cummings 2012, Willink et al. 2013), crab-spiders (Théry & Casas

2002, Heiling et al. 2005, Théry et al. 2005), and venomous snakes (Niskanen & Mappes 2005). Despite insects being a major food source for birds (The Birds of North America N.D.), relatively few studies have considered their visual appearance outside the confines of the human visual spectrum. Of these, most have examined how UV signals in Lepidopteran dorsal patterns impact avian predator decisions (i.e., Remington 1973, Lyytinen et al. 2004, Olofsson et al. 2010).

These, among other studies, suggest that visual contrasts are important for prey discrimination by birds. Visual contrasts between objects can describe either differences in color intensity (achromatic contrasts) or differences in hue and saturation (chromatic contrasts) (Kelber et al. 2003). Chromatic and achromatic contrasts are processed differently by birds (Osorio et al. 1999, Jones & Osorio 2004). For instance, Osorio et al. (1999) found that foraging domestic chicks use chromatic contrasts to detect large objects whereas achromatic contrasts are used to distinguish small objects. Some examples of avian predators using visual contrasts to detect insect prey are discussed below.

I aim to add to the current literature by investigating how visual appearance of beetle prey determined in avian vision space simultaneously impact predator and prey abundance in a multitrophic community. In this study I consider a color pattern to be *cryptic* if it "minimizes the probability of detection against the visual background" or *aposematic* if it is "conspicuous and aids the predator to identify the prey as carrying a defense worth avoiding" (Endler 1988), thus is similar in appearance to a harmful animal. My community of interest consists of woodboring beetles (Family Cerambycidae), their generalist beetle predators (Families Cleridae, Cucujidae, Histeridae, Passandridae), and insectivorous forest birds. These forest beetles have either cryptic or aposematic

patterns; many within the latter category resemble Hymenoptera in both appearance (to a human) and behavior (Linsley 1959, Mawdsley 1994). This resemblance, at least at longer wavelengths, may influence both beetle and bird populations due to bird preferences. For instance, Jones (1934) observed that when offered an assortment of insects with variable appearances, birds preferred cryptic- over aposematic-patterned prey. However, other studies have found that visually apparent insect patterns with high chromatic contrast may reduce survival (Stobbe & Schaefer 2008). Furthermore, prey's reflectance at shorter wavelengths may have various outcomes on predation. In some cases UV reflectance may actually attract birds to their insect prey (Lyytinen et al. 2004) or may deflect predator attacks to specific regions of the prey's body less crucial for survival (Olofsson et al. 2010).

If visual contrasts are important for prey detection leading to predation, variations in visual contrasts of beetles with backgrounds moderate the degree to which bird abundance impacts beetle abundance (Figure 5.2). Under this scenario, I predict that bird abundance will be correlated with abundance of beetles with high visual contrasts with forest substrates (i.e., lichen, bark, leaves) (not cryptic) or wasps (not aposematic). I also expect that visual contrasts are less important for flycatching birds because their hunting strategy focuses on locating aerial prey from a distance rather than foraging prey from substrates (Fitzpatrick 1980, Fitzpatrick 1981). Therefore, considering that contrasts of prey may not be important, flycatchers will depredate equally across contrast groups.

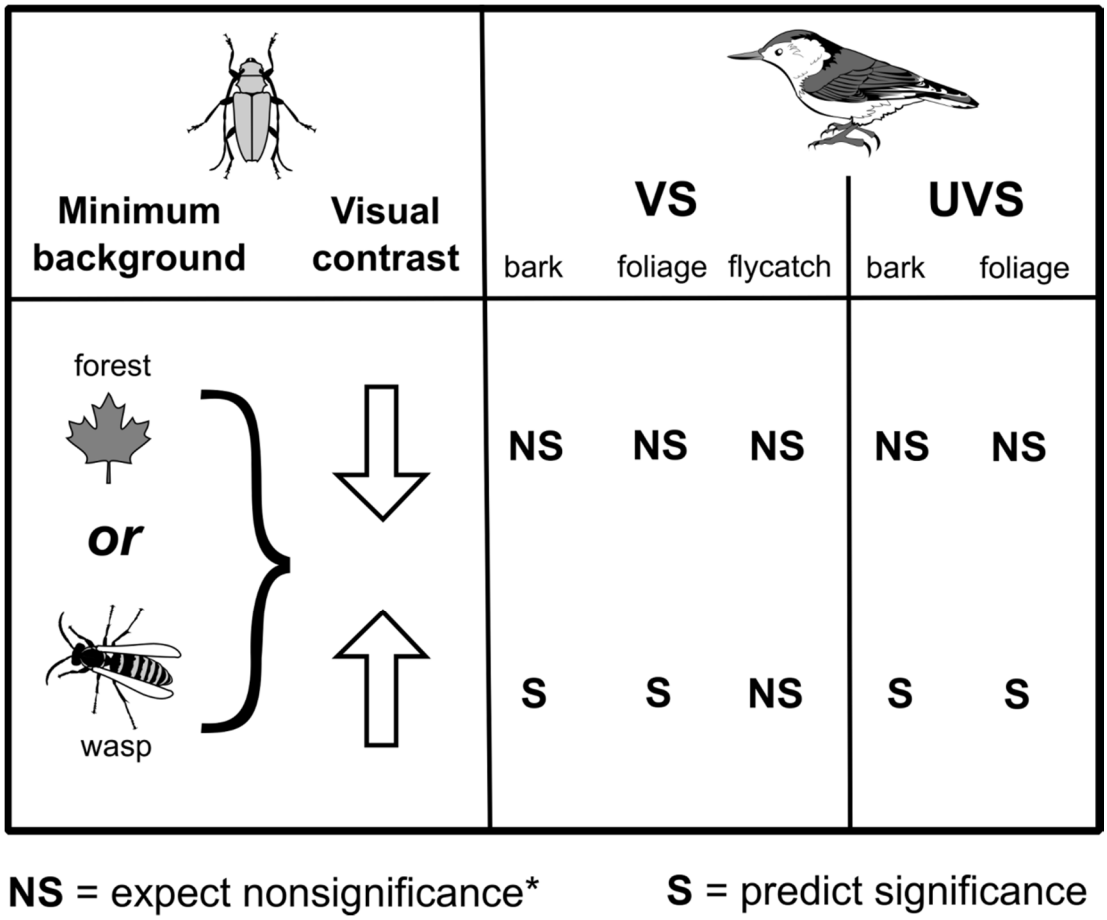

Figure 5.2: My predictions of vision-mediated interactions between birds and beetles. I predicted significant (S) correlations between the abundance of birds that glean substrates and the abundance of beetles that are not "cryptic" (similar to forest backgrounds) and not "aposematic" (similar to a wasp). *All other relationships are given a status of "nonsignificance (NS)" as a default.

To test these predictions, I use the model proposed by Vorobyev et al. (1998) described in Chapter 2 to compare insects against 1) common forest backgrounds and 2) other insects having long-wave aposematic patterns in order to examine the insects' visual appearance strictly within the tetrachromatic vision space of their avian predators (Figure 5.1). Under this premise, insects can be classified as highly conspicuous or cryptic based on how similar the insect's patterns are against these visual backgrounds. I

then use visual contrasts of beetles within these classifications to link predator and prey trophic levels and thus simultaneously examine changes in predator and prey abundances.

5.2 Methods

5.2.1 Beetle and bird collection

Wood-borer beetles (Coleoptera: Cerambycidae) and their beetle predators (Coleoptera: Cleridae, Cucujidae, Histeridae, and Passandridae) were sampled at 18 sites along a forest fragmentation gradient in Indiana, USA. The forest habitat was secondary growth forest fragmented by agricultural and urban land use. The range of the fragmentation gradient measured at a 2 km radius was from 100% to approximately 5% forest. Beetles were trapped within each site using one Lindgren multiple funnel trap (12 funnel size; Phero Tech, Delta, Canada), one Intercept panel trap for bark beetles (Integrated Pest Management Tech, Portland, OR), and one multi-pane window trap, all baited with 99% ethanol (Holland 2006). Trapping lasted 70 – 90 d over the summers of 2006 and 2007. Wood-borers and predator beetles were identified to species using Yanega (1996), Linsley (1962a, b, 1963, 1964), Linsley & Chemsak (1972, 1976), Arnett et al. (2002a, b) and Downie & Arnett (1996a, b). All specimens were deposited into the Landscape Ecology and Biodiversity laboratory at Purdue University.

Birds were previously surveyed across the sites from which beetles were collected during the summers of 2001 – 2003 using the double-observer (Nichols et al. 2000), fixed-radius (Ralph et al. 1995) point count technique. Birds were counted in two three-minute segments for a total of six minutes per point. Birds were counted by species within a fixed point in the center of 50-m radius circles in wooded habitat. Each point

was surveyed twice during the summer season and between sunrise and 10:00 AM. I included in the data analysis only birds detected within this plot that were known to be primarily insectivorous during summer months and are summer residents of Indiana hardwood forests.

5.2.2 Beetle visual contrasts

I selected insect specimens from the reference collection in the laboratory and the Purdue Entomological Research Collection (PERC). The most recently curated specimens within species were used. Where sexual dimorphism was present within a beetle species, I chose only female beetle specimens because predation upon females will have a more direct effect on the population than predation upon males. Many species of beetles in my dataset resemble Hymenoptera (Linsley 1959, Mawdsley 1994). Therefore, I included wasp species common to Indiana forests to compare beetles to these proposed mimicry models in avian tetrahedral color space (Appendix L). For eusocial hymenoptera species, I preferred worker castes for visual contrast analysis because they are more likely to be encountered by avian predators. I also collected digital images of the dorsal surfaces of beetles and wasps with a LeicaM165 C microscope and LAS V4 version 4.2 software for image stacking.

To construct visual contrasts, I obtained reflectance spectra (beetles, wasps, and common forest visual backgrounds) using a StellarNet Black Comet C-50 portable spectroradiometer (StellarNet-Inc., Tampa, FL). Measurements were recorded at 0.5 nm intervals from 300 to 700 nm using a micron fiber optic probe and a combination Tungsten Krypton and Xenon light source. I measured beetles and wasps in a small dark

chamber. The probe was held at a constant 45º angle with the light shining in the direction of the insect's dorsal surface from a distance of 4 mm. For all species, reflectance spectra from four representative individuals were recorded using an integration time of 300 ms and averaging every 3 scans. As specimen size permitted, I took three measurements from various regions of the insect body including the head, pronotum, and elytra for beetles and the pronotum and gaster for wasps.

I collected representative samples of visual backgrounds from the Ross Biological Reserve in Tippecanoe County, IN, USA (40.41°N, 87.07°W, WGS84). These backgrounds included tree bark, moss, lichen, and leaves of species common to Indiana forests (Appendix L). I selected these backgrounds because they are frequent foraging sites for birds (Jackson 1979) and because they are common substrates within the habitat of the cerambycids (Linsley 1961) and the beetles that are their predators (Böving and Champlain 1920, Ulyshen et al. 2004) in my dataset. I made ten measurements of each background type including dorsal and posterior surfaces of leaves with the probe at a constant 45º to the object. Measurements were made with an integration time of 1000 ms and averaging every 10 scans. Spectra were averaged across plant part (dorsal and ventral surfaces of leaves and bark, lichen, and moss) measured at each wavelength to yield one average spectrum per background plant part.

Before averaging spectra from insects or backgrounds, I manually smoothed curves to remove the peak artifact at 650 – 655 nm produced by the deuterium lamp as part of the spectroradiometer apparatus. At each wavelength I averaged spectra across body region to yield one average spectrum per species. I then calculated a percent reflectance spectrum for each average spectrum. For insect species large enough for

multiple regions to be measured, I weighted percent reflectances from each body region based on the percent area of that region made of the entire insect body. I obtained the percent areas with ImageJ (Schneider et al. 2012). White and dark references were taken before measuring each species and background. The white standard had reflectivity > 98%. The dark reference was measured by placing the probe against the white standard with no light source.

The visibility of color patterns in relation to backgrounds may differ under different environmental light conditions (Endler 1987, Endler 1993, Fernández-Juricic et al. 2012). Therefore, ambient light was measured among sites selected to represent a spectrum of forest light conditions: closed canopy, small gap, and large gap (for details, Moore et al. 2012). The irradiance data were collected on August 25, 2014 at some of the beetle collection sites within the Morgan-Monroe State Forest, Indiana with a JAZ-ULM-200 irradiance module and an Ocean Optics Jaz Spectrometer. Data acquisition was restricted to 9:00 – 11:00 AM on a day with no cloud cover, conditions favoring the foraging of diurnal, insectivorous birds (Hutto 1981, Bednekoff & Houston 1994).

I used the percent reflectance and irradiance data in the R package pavo (Maia et al. 2013, R Core Team 2014) to construct chromatic (dS) and achromatic contrasts (dL) between 1) beetle species and wasp species and 2) between beetle species and backgrounds (Figure 5.3). Contrasts were made considering the three light conditions with two average bird models for the violet-sensitive (VS) system and the ultraviolet-sensitive (UVS) system (Cazetta et al. 2009, Stoddard & Stevens 2011) with the package "pavo" (Maia et al. 2013, R Core Team 2014). I used these two models because avian

species have visual sensitivity to the ultraviolet (approximately 355 – 400 nm) or violet (approximately 400 – 426 nm) spectrum (Hart 2001).

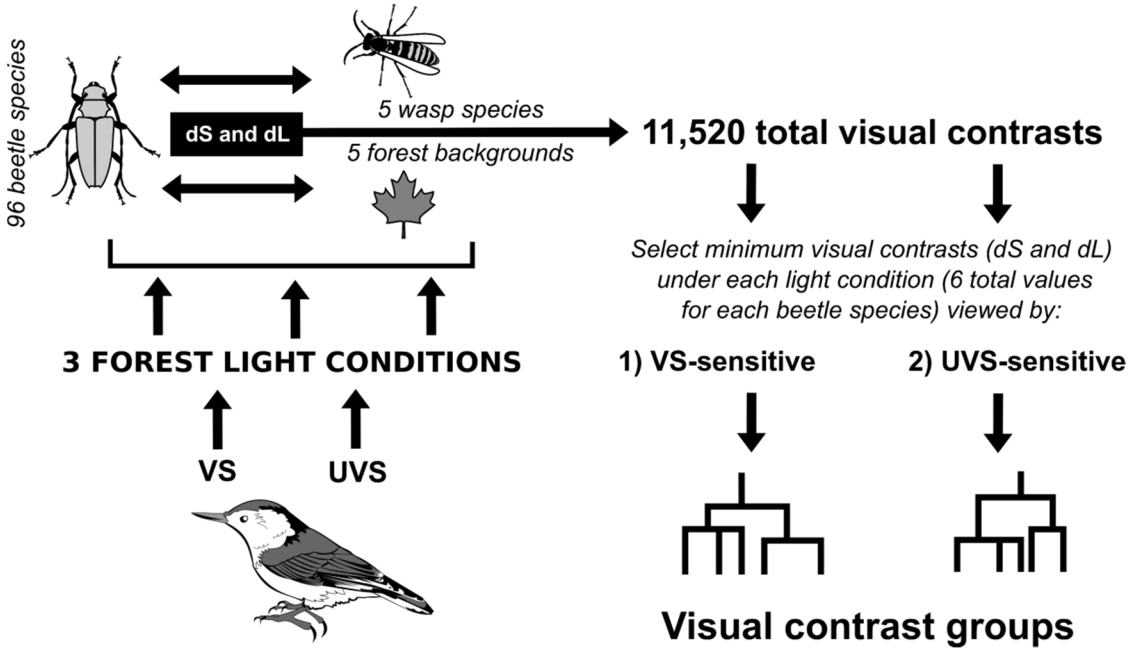

Figure 5.3: Flowchart illustrating methods to obtain visual contrast groups. Chromatic (dS) and achromatic (dL) contrasts were made between ninety-six beetle species and 1) five wasp species and 2) five forest substrates (top and bottom of leaves, bark, lichen, moss). These contrasts were calculated under three forest light conditions (closed canopy, small gap, and large gap) and two average avian visual systems, violet-sensitive (VS) and ultra-violet sensitive (UVS).

5.2.3 Beetle visual contrast groups

I selected the minimum visual contrasts (dS and dL) for each beetle species with forest or wasp backgrounds under each light condition under the average UVS and VS bird models. This gave a total of 6 values for each beetle species: 3 dS and dL distances within the tetrahedral color space of 1) birds with VS cones and 2) birds with UVS spectral tuning. I used cluster analysis of the Euclidean distance of these values to group beetles into visual contrast groups based on minimum contrasts with backgrounds. Scree

plots were used to determine the pruning height of the dendrograms to obtain "visual contrast groups." Members of beetle visual contrast groups are given in Appendix M.

5.2.4 Avian assemblages (Appendix N)

Birds may have one of two types of short-wave sensitive (SWS1) cones, UVS or VS which may be determined through the sequencing of the SWS1 opsin gene (reviewed in Chapter 2). I made bird visual system estimates (VS or UVS) for species in my dataset based on findings from Bennett & Cuthill (1994), Ödeen & Håstad (2003), Ödeen et al. (2011), Aidala et al. (2012), and Ödeen & Håstad (2013). Similar approaches have been made by Stoddard & Stevens (2011). I further divided birds within VS and UVS groups based on their foraging habits (gleaning leaves, gleaning bark or flycatching) (The Birds of North America N.D.) to obtain final groups henceforth called "avian assemblages." I performed analyses using species abundance within beetle visual contrast groups, VS and UVS groups, and avian assemblages (below). Members of avian assemblages are given in Appendix N.

5.2.5 Analysis

I removed a total of 51 beetle species (<=5 total individuals/species for beetles) and 9 bird species (<=10 total individuals/species for birds) (Appendix O, Appendix P). I performed redundancy analysis (RDA) using abundance of beetle species within beetle visual contrast assemblages as response variables and bird abundance within avian assemblages as predictor variables. I tested the significance of these relationships with permutation tests. One avian assemblage contained only one species, the yellow-billed

cuckoo (YBCU), *Coccyzus americanus*. Correlations in these triplots were skewed due to containing only one predictor variable. Therefore, I performed RDA with this single predictor but conducted correlation tests between *C. americanus* and beetle species to examine their relationships.

5.3 Results (Fig. 5.5)

A total of 73 species of longhorned beetles and 23 species of predator beetles were collected (Appendix O), and 48 species of insectivorous birds that are summer residents in Indiana hardwood forests were recorded (Appendix P). Cluster analysis on the minimum contrasts selected under each light condition (six total values each for UVS and VS visual models) revealed four VS visual contrast groups and three UVS visual contrast groups (Figure 5.4). Visual contrast groups were clearly discriminated by how visually apparent beetles are to their avian predators based on chromatic and achromatic contrasts against wasps and common forest backgrounds. VS visual contrast group 3 (VS.3) and UVS visual contrast group 2 (UVS.2) had high acromatic and chromatic contrasts thus would be most visually apparent to birds.

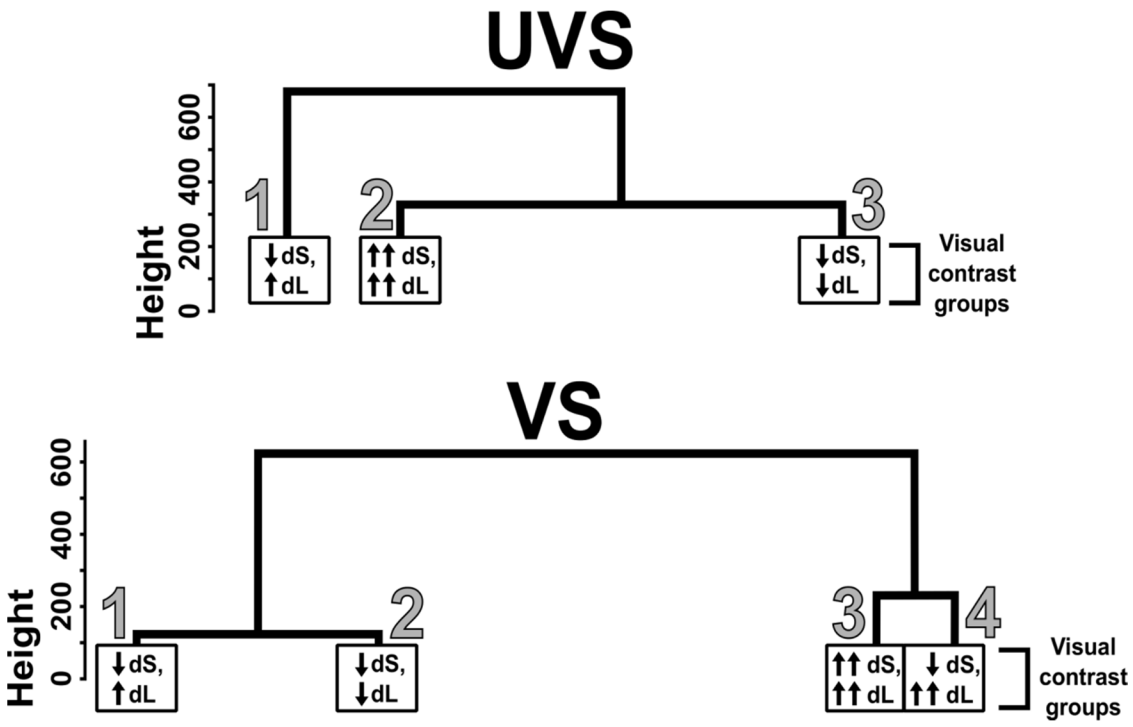

Figure 5.4: Beetle visual contrast groups (under ultraviolet-sensitive (UVS) and violet-sensitive (VS) bird models). Groups are defined by chromatic (dS) and achromatic (dL) contrasts with substrates. The direction of the arrows indicates whether the beetle has high or low contrast with substrates. Groups with double arrows have very high dS or dL values.

Predictions were supported for all scenarios other than for birds with UVS-sensitive cones (Figure 5.5). I found that visual contrasts of prey were important for birds with VS cones that glean bark ($p = 0.015$) (Figure 5.6). Within VS visual contrast group 3, a beetle group that is visually apparent to birds with VS cones, the predator beetle *Catogenus rufus* was positively correlated with the pileated woodpecker, *Dryocopus pileatus* (PIWO), while the predator beetle *Platysoma aurelianum* was negatively correlated with the red-bellied woodpecker, *Melanerpes carolinus* (RBWO). I

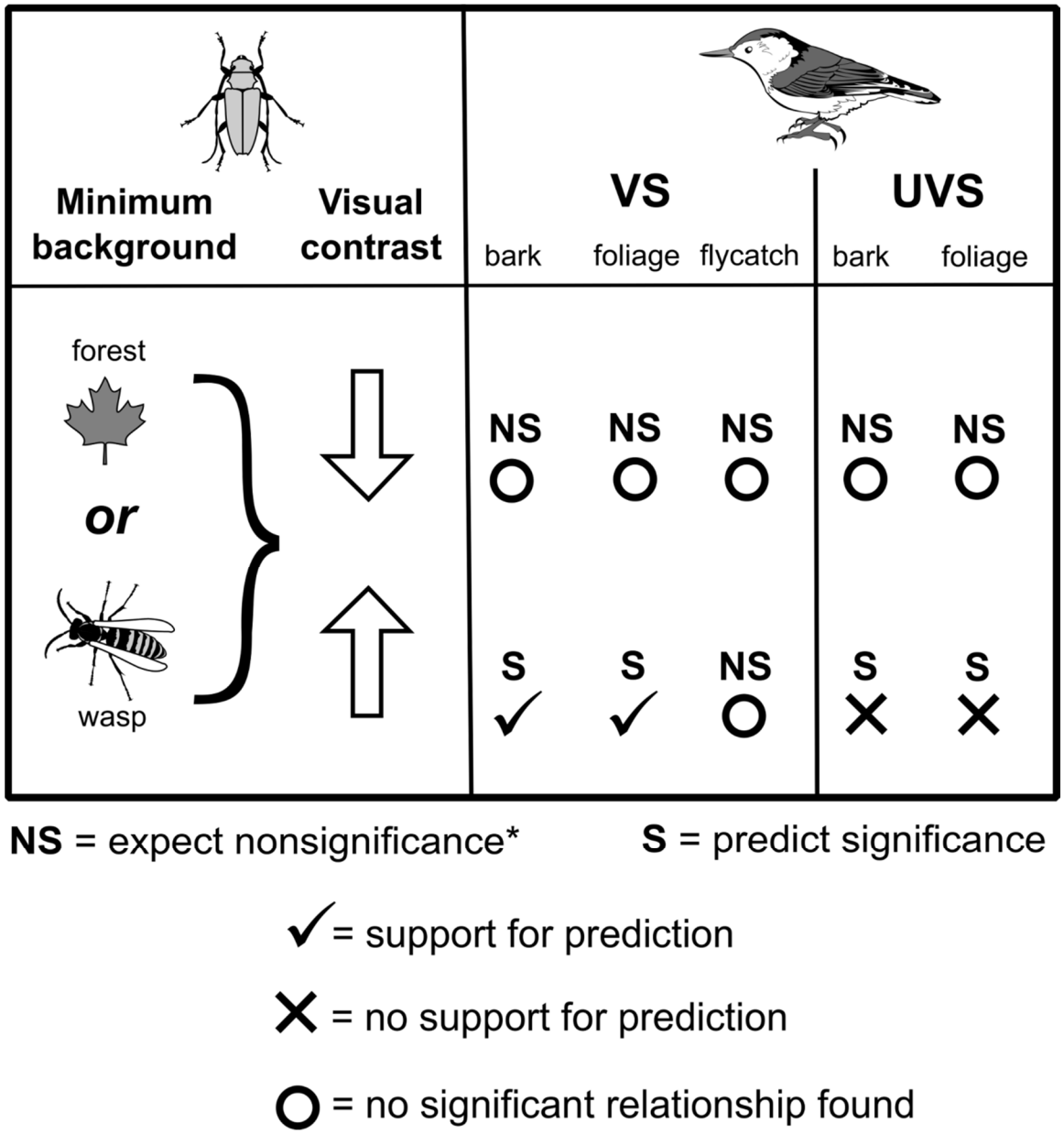

Figure 5.5: Summary of results. I predicted significant (S) correlations between the abundance of birds that glean substrates and the abundance of beetles that are not "cryptic" (similar to forest backgrounds) and not "aposematic" (similar to a wasp). *All other relationships are given a status of "nonsignificance (NS)" as a default. My predictions were supported with substrate-gleaning birds with a violet-sensitive (VS) visual system but not for substrate-gleaning birds with an ultraviolet-sensitive (UVS) visual system.

did not find strong correlations of two other visually apparent beetles, *Aegomorphus modestus* or *Gaurotes cyanipennis* with any birds gleaning bark and having VS cones.

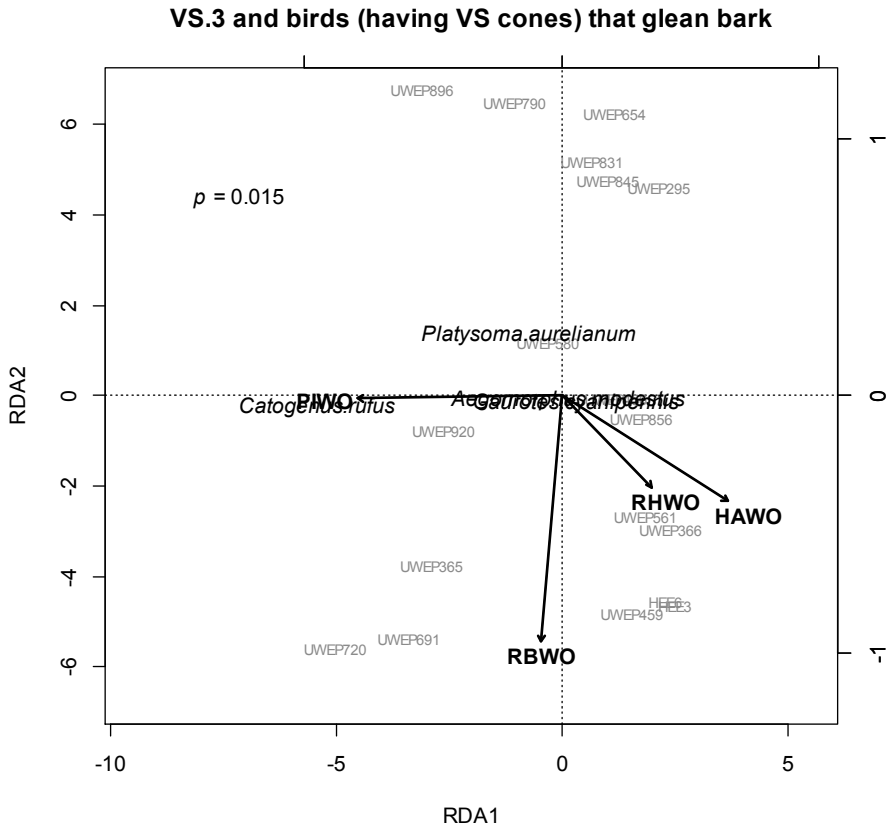

Figure 5.6: Example of a redundancy analysis (RDA) triplot. This is one example of 18 bird-beetle triplots. This plot shows beetle visual contrast group 3 (under a VS bird model, thus VS.3) and birds (with estimated violet-sensitive (VS) vision) that glean bark.

I found that visual contrasts of prey were important for the yellow-billed cuckoo, *Coccyzus americanus* (YBCU), a bird estimated to have VS spectral tuning and that commonly gleans leaves. Although the overall relationship between the cuckoo and the highly visible beetle VS visual contrast group 3 (high chromatic contrast, high achromatic contrast) was significant ($p = 0.04295$), no correlation was found between

individual beetle species and this bird (Figure 5.7). I also found that visual contrasts are not important for flycatching birds with VS cones. Specifically, I did not find a significant relationship between VS visual contrast group 3 and flycatching birds with VS cones. However, I did find a significant relationship ($p = 0.026$) between VS visual contrast group 4 (VS.4, low chromatic contrast, high achromatic contrast with minimum background) (Figure 5.8) and flycatchers. But, the strength of the correlations was not strong between individual beetle species and bird species. Furthermore, beetles in this

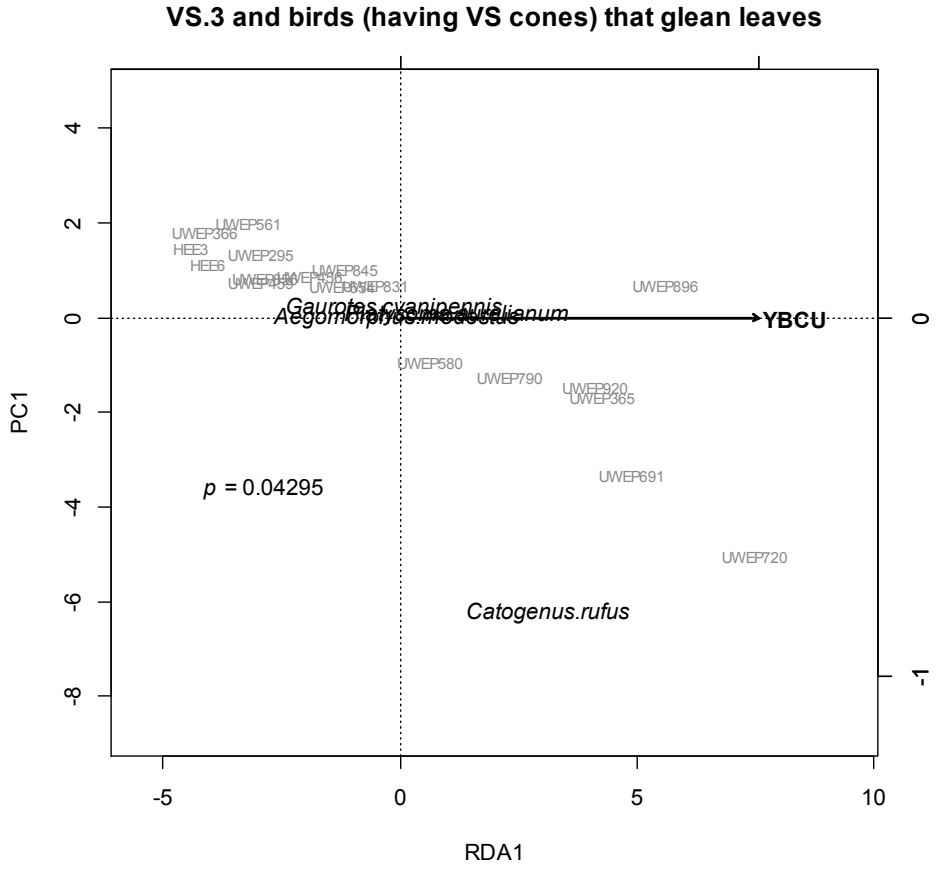

Figure 5.7: Example of a redundancy analysis (RDA) triplot. This is one example of 18 bird-beetle triplots. This plot shows beetle visual contrast group 3 (under a VS bird model, thus VS.3) and birds (with estimated violet-sensitive (VS) vision) that glean leaves.

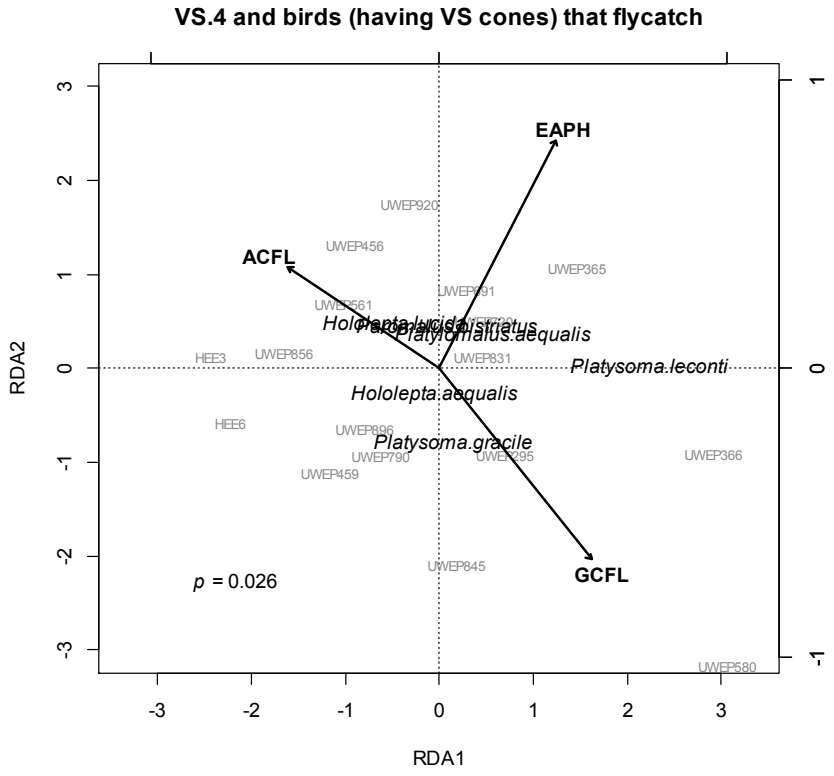

Figure 5.8: Example of a redundancy analysis (RDA) triplot. This is one example of 18 bird-beetle triplots. This plot shows beetle visual contrast group 4 (under a VS bird model, thus VS.4) and birds (with estimated violet-sensitive (VS) vision) that flycatch.

contrast group are primarily found under bark and in galleries so would not commonly be encountered by flycatching birds.

I did not find any significant relationships between UVS visual contrast groups and birds with UVS cones. I wished to investigate whether visual contrasts were important for these birds. I selected three species that glean leaves, 1) Baltimore oriole, *Icterus galbula*, 2) blue-gray gnatcatcher, *Polioptila caerulea*, and 3) warbling vireo, *Vireo gilvus*, and one species that gleans bark, the white-breasted nuthatch, *Sitta carolinensis,* and used these as single predictor variables in RDA with beetle visual

contrast groups. I tested the significance of these relationships with permutation tests. No relationship between visual contrast groups and these bird species was significant.

5.4 Discussion

This is the first study to use visual contrasts to examine the interplay between predator and prey abundances in a multi-trophic community. I found that variations in visual contrasts of beetles with backgrounds do moderate the degree to which bird abundance impacts beetle abundance with birds that have a VS visual system and forage on substrates. The strongest correlations were found when the foraging habitat matched that of both beetle species within visual contrast groups and bird species within bird assemblages. I expected that visual contrasts would have little impact on beetle abundance with birds that flycatch considering that these birds forage for prey at a distance, a strategy that relies on prey movement and not strongly on visual contrasts. With respect to the relationships involving flycatching birds, no significant relationship was found except when comparing beetles with low chromatic contrasts but high achromatic contrasts. Contrary to my predictions, visual contrasts of beetles did not moderate the degree to which bird abundance impacts beetle abundance when considering birds that have a UVS visual system. These results suggest that UV reflectance and visual contrasts of insects have multiple roles in the signaling to a community of avian predators.

I developed new methodology to use prey visual contrasts to link trophic levels in order to examine the interplay between predator and prey abundances. Interestingly, the association had better resolution when I compared beetle and bird species that utilize

similar forest habitat as part of their functional roles. The insectivore birds in my study are generalist predators that demonstrate prey switching behavior. Under this behavior, if one insect becomes more common, birds will switch and depredate it (Murdoch 1969). Considering this lack of specialization, strong correlations between individual insect and bird species would not be expected. This is actually what I observed for the majority of relationships, except for when beetles and birds shared a similar foraging habitat. Interestingly, with the latter relationships, I observed strong correlations between the abundance of visually apparent beetles and the abundance of birds. This indicates that species' functional roles, rather than species-species correlations, must also be important for detecting predator-prey interactions in communities. Therefore, I suggest that this approach should not only link trophic levels with vision-mediated predator-prey interactions but include a species functional link as well.

I found significant correlations between abundances of highly visible beetles and birds with VS spectral tuning that glean substrates. These results are in accord with previous studies indicating that visual contrasts are important for avian predators. Overall, these relationships were strongest when birds and beetles rely on the same forest resources. The birds in the VS avian assemblage that glean bark consisted of woodpeckers, and the predacious beetles with the strongest relationship with woodpeckers, *C. rufus* and *P. aurelianum*, are commonly found in dead or dying wood (Bousquet & Laplante 2006, Evans 2014) (Figure 5.6) and were among the most abundant beetles in my dataset. No previous study has examined a woodpecker's retina via microspectrophotometry techniques, but I estimated that the SWS1 cones of these birds have violet sensitivity based on the sequencing of the European green woodpecker,

Picus viridis, another member in the Picidae (Ödeen & Håstad 2013). Regardless of avian visual system, I found that these beetles are highly visible against common forest backgrounds and wasps, both with respect to chromatic and achromatic contrast. Therefore, I would expect that these insects are very likely to be encountered, visually detected, and depredated by foraging woodpeckers.

Two other beetles that were highly visible to birds with a VS visual system, *G. cyanipennis* and *A. modestus* (Figure 5.9) were not correlated with any bird regardless of the bird's visual system. *G. cyanipennis* has a metallic green appearance (to humans) plus UV reflectance (to birds) and is commonly found on flowers as an adult, not in larval host logs (Lingafelter 2007). Therefore, I expect that there is a low encounter rate between this beetle in its adult form and woodpeckers due to them being common in different forest micro-habitats. Another cerambycid beetle, *A. modestus*, has a dorsal pattern appearing similar to bark or lichen under long wavelengths which may camouflage this nocturnal beetle from predators during the day. However, I found that this beetle's pattern has a UV component, and the tetrachromatic models indicated that this beetle would be apparent to birds having either UVS or VS visual systems. The lichen measured in my study did not have UV reflectance, but interestingly, certain lichens in temperate forests do (Majerus 2000). The pigments of chlorophyll contain chlorophylls, xanthophylls, and cartenoids that absorb light with UV, blue and red wavelengths (Roy 1989). Similarly, all parts of foliose lichens considered in a study by Majerus (2000) absorbed UV light. However, parts of certain lichens, in particular,

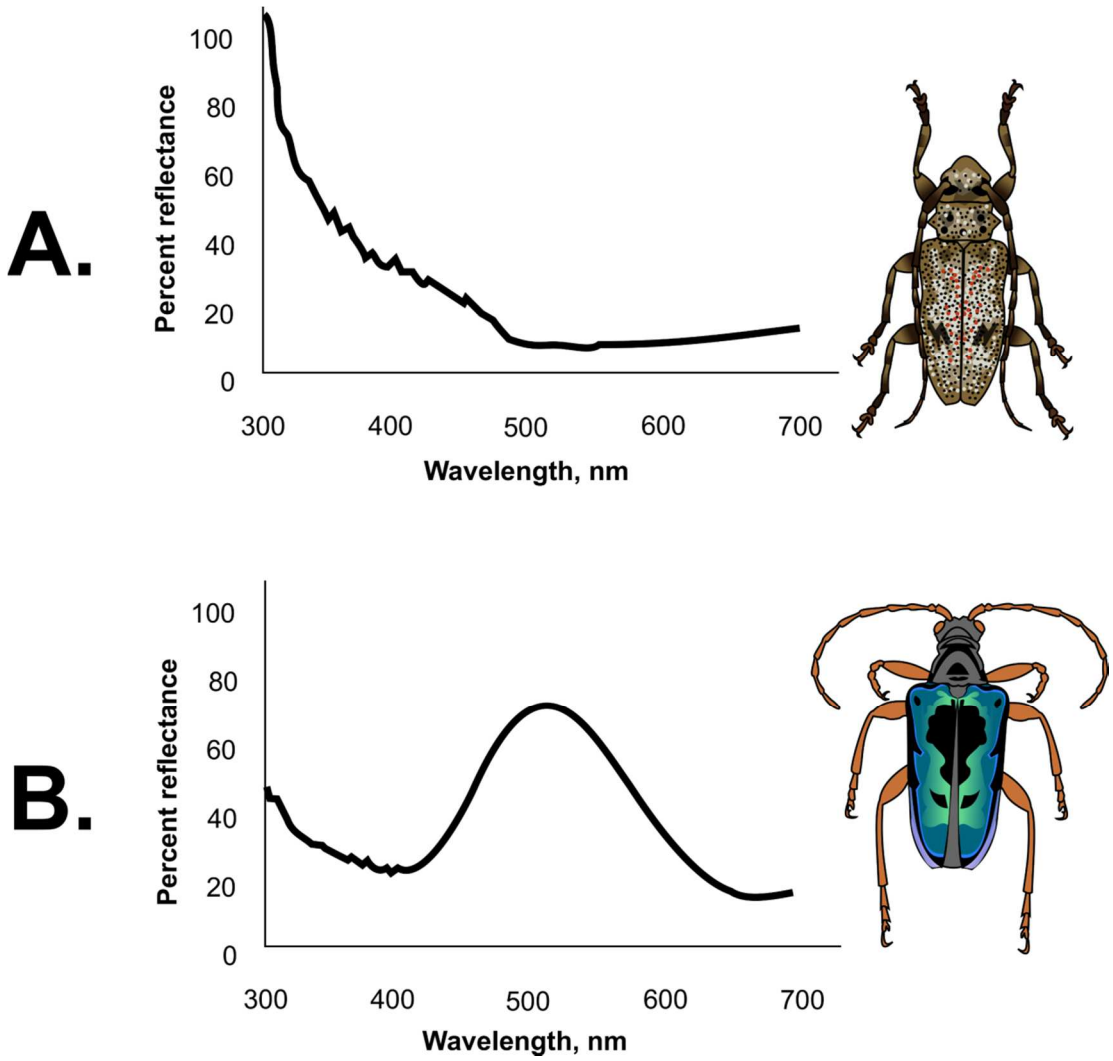

Figure 5.9: Reflectance spectra of A) *Aegomorphus modestus* and B) *Gaurotes cyanipennis*, two visually apparent beetles to birds regardless of avian visual system.

crustose lichens, reflect UV light (Majerus 2000). Therefore, this variation in UV reflectance and absorbance may give certain lichens a mottled UV pattern to avian predators. I did not test this here, but I expect that under certain lichen backgrounds, the UV reflectance of this beetle contributes to the cryptic coloration under short wavelengths making it camouflaged from avian predators like woodpeckers, although future investigation would need to be conducted to confirm this. In addition to the lack

of encounter or detection of these beetles by woodpeckers, I expect that the weak relationship between these beetles and birds is also due to their low relative abundance compared to other beetle species which would further compound the low encounter rate of these beetles by birds (Charnov 1976).

I also found a marginally significant relationship between the yellow-billed cuckoo, a leaf-gleaning bird estimated to have VS spectral tuning, and beetles highly visible to the VS visual system. However, there was no correlation between individual beetle species and this bird (Figure 5.7). The adult habitat of these beetles (discussed above) is not similar to the common foraging substrate of the cuckoo thus would also not be as likely to be encountered by this bird.

Flycatchers detect their prey from a distance (Fitzpatrick 1980, Fitzpatrick 1981) thus may rely more on motion rather than visual contrasts to identify insect prey. Currently, no published microspectrophotometric data on a flycatcher's retina exist, but eye physiology is well adapted to foraging strategy in many animals examined thus far, including birds (reviewed by Osorio & Vorbyev 2005). Interestingly, Capenhousen and Kirschfeld thought that the double cone photoreceptors in the avian retina are used in motion detection (as cited in Hart 2001) and are also used to discriminate achromatic contrasts (Jones & Osorio 2004) (reviewed in Chapter 2). Furthermore, achromatic contrasts may be important for the identification of small objects whereas chromatic contrasts are used to detect large objects (Osorio et al. 1999). I found a significant correlation between flycatchers and beetles having low chromatic contrast and high achromatic contrast (Figure 5.8), but no beetle in this visual contrast group was significantly correlated with any bird in the bird assemblage group. The primary habitat

of all the adult beetles in this visual contrast group is located under bark or in galleries of dead or decaying wood (Drooz 1985, Downie & Arnett 1996a, b, Bousquet & Laplante 2006, Evans 2014). Therefore, these beetles are unlikely to come in regular contact with flycatchers unless leaving deadwood by flight to find new oviposition or foraging sites. These results are intriguing, however, particularly considering the common role of detecting motion and achromatic contrasts by double cones in the avian retina. Future directions could collect specific data on the flycatcher's retina to determine whether it contains a high proportion of double cones and the visual acuity to distinguish visual contrasts from a distance. Small prey items with high achromatic contrast would be very visually apparent to birds with these adaptations.

Multiple studies have demonstrated that UV reflectance is an important signal to birds with UVS vision (Cuthill et al. 2000). But contrary to my predictions, I did not find any significant relationships between beetle visual contrast groups and bird assemblages with UVS spectral tuning regardless of beetles' chromatic and achromatic contrast values. I expect that this is due to differing roles that UV signals have to avian predators. To date several important purposes of UV reflectance in insect patterns have been discovered. Cuthill et al. (2000) suggest that the UV component of a pattern may serve as part of an aposematic signal. For instance, one study that investigated reflectance of lepidopteran larvae found that one species that appears green to humans, *Lithophane ornitopus*, actually has a UV component to its pattern suggesting that this larvae is visually apparent rather than cryptic against non-UV reflecting twigs and foliage (Church et al. 1998). Other findings suggest that the eyespot pattern on the wings of the moth, *Lopinga achine*, contains a highly visible UV component which serves to deflect predator

attacks to less important body regions (like away from the head and to distal regions of wings (Olofsson et al. 2010). UV reflectance may not always benefit an insect, however. For instance, patterns with high chromatic contrast (potentially created by UV reflectance) has been shown to reduce prey survival rates (Stobbe & Schaefer 2008), and in some cases UV reflectance may actually attract birds to their insect prey (Lyytinen et al. 2004). These studies have strictly used lepidopteran models, and to my knowledge the role of UV reflectance in patterns has not been directly investigated in beetles. But considering that beetles are also major food items for birds, it is likely that such mechanisms are also present in members within this highly diverse insect group.

The methods developed here emphasize the importance of species' function for giving greater resolution to relationships between predator and prey abundances. I suggest that correlations between predator and prey be limited to organisms that have some functional overlap (i.e., in this study, forage in dead or dying wood). Findings from this new methodology support that visual contrasts are important in vision-mediated predator-prey interactions. This approach is highly transferable across a wide range of communities given that the visual system of the predator is known and the appropriate measurements of prey and light conditions under which the prey is viewed may be made. Many data have been acquired and are available for many other predator-prey systems via other studies using visual contrasts, and species' functional roles can be acquired from numerous sources (Chapter 3). Future directions may consider other multi-trophic systems.

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CHAPTER 6. CONCLUSIONS

6.1 Conclusion

My overall objective in this study was to examine change in a multitrophic community resulting from habitat fragmentation. To do this, I decided to use functional diversity as an indicator of change, and the community of choice consisted of longhorned beetles, their generalist beetle predators, and diurnal insectivore birds. I also aimed to determine which, if any, ecological stability mechanism was operating to buffer the beetle community from disturbance. The considerations of predator-prey interactions were also important for this study, thus, I also wanted to investigate how predator abundance impacts prey abundance and vice versa at the community level.

These research objectives were met, but there were several challenges in the process. First, functional diversity may be a better indicator for ecosystem change than biodiversity, but most previous studies that have investigated community change at the functional diversity level classified species into functional groups with very few functional traits. This approach, either appropriate for certain research objectives or unavoidable because of a lack of ecological knowledge on species, may consequently produce functional groups that do not entirely represent species' functional diversity. Also, simultaneous changes in functional diversity of a multitrophic community had not been previously examined. With respect to detecting ecosystem stability

mechanisms, there was already an outline for detecting cross-scale resilience, but this approach just considered the single best focus at which species best respond to changes in landscape pattern. I wished to produce an ecologically relevant measure of detection, so I included how species respond to the landscape along the entire trend of ecologically relevant foci. Another main challenge I encountered was developing new methodology to link trophic levels to examine how avian predator and beetle prey abundances impact one another across an entire community. This was something that, to my knowledge, had not been attempted previously.

There were several approaches that I developed to meet these challenges. One was to capture the entire known functional spectrum of the species to acquire functional groups that best predict beetle species' functional roles in the community. To do this, I obtained as much ecological knowledge on the beetles as possible through literature sources. I also developed two novel functional traits, landscape response and avian visual perception of beetles, to better capture species' functional roles. Landscape response was determined by the response of species to landscape patterns across all species-relevant foci to produce landscape response trends. These response trends were informative for determining how species respond across the entire landscape relevant to their ecology (i.e. dispersal and foraging behavior), and not just a single landscape focus. I developed another novel functional trait, avian visual perception, which linked predators and prey in functional trait space by considering vision-mediated avian behavior.

Another main challenge was to determine how to examine simultaneous change in prey and predator functional diversity. This was particularly difficult in my study

considering that I assessed changes in functional diversity in response to habitat loss and fragmentation measured across multiple analytical foci. I selected the landscape metric measured at the analytical focus with the best explanatory power for predator beetle and longhorned beetle functional diversity to produce three-dimensional surfaces of community-level functional diversity. This curve indicated which landscapes were best for promoting the functional diversity of this community.

The concept of landscape response trends was further developed to detect one ecological stability mechanism, cross-scale resilience, in this research study. I obtained these trends for each beetle species and then grouped species based on trend similarity. To detect cross-scale resilience, I examined the distribution of species with similar ecological function across landscape trends. Cross-scale resilience could be operating in this community because species with similar function also had different landscape response trends.

One of the main challenges of this study was how to best assess predator-prey interactions in this multitrophic community. I took a similar approach to the development of the avian visual perception functional trait (which used visual contrasts of beetle prey) to directly examine changes in predator and prey abundance. I grouped beetles into visual contrast groups according to how cryptic or apparent they were to their avian predators. I also grouped bird species according to the spectral tuning of their short wave sensitive cones (UV-sensitive or violet-sensitive) and then further grouped them by foraging guild which yielded avian assemblage groups. I directly compared the abundance of beetle species within beetle visual contrast groups to abundance of bird species within avian assemblages. I found that that vision-mediated behavior impacted

this community, but to make the link, it was important to incorporate avian and beetle ecological function.

I found that changes in longhorned beetle functional diversity represented by functional richness was more negatively impacted by fragmentation than predator beetle functional diversity at the community level. These results did not support my predictions. However, at the functional group level, in accordance with my predictions, the response diversity and functional redundancy of predator beetle and wood-borer functional groups were generally reduced in fragmented landscapes. Among wood-borers, this trend was observed within functional groups that had the most diverse trait profiles. Also supporting my predictions, I found that functional diversity assessed at both the community and functional group levels of wood-borers and their predators exhibited a threshold response to fragmentation. This indicated that the functional diversity of the community was stabile along the gradient but past a threshold of fragmentation began to suddenly change.

Functional richness at the community level is equivalent to the convex hull volume of the community's functional trait space (Villéger et al. 2008) and is therefore a measure independent of species abundance. I examined changes at the functional group level with functional redundancy and response diversity. Whereas functional redundancy was simply the number of species within functional groups, response diversity was assessed using the functional diversity index, functional dispersion (FDis). Functional dispersion was a measure of within-functional group dispersion in trait space and incorporates species abundance and its distribution within functional trait space. When functional dispersion is high, species' with high abundance are more dissimilar within the

group. But, when functional dispersion is low, abundance is greater among species with trait values closer to the average trait values of the group.

My results at community and functional group levels are consistent in that wood-borer functional richness, functional redundancy, and response diversity all decreased with habitat fragmentation. Therefore, for wood-borers, fragmented landscapes harbored fewer species that had similar functional trait profiles. The overall trend was less clear with the predator beetles since I only found correlation between one predator functional group and landscape and I did not detect any trends on how functional redundancy of predator functional groups changed with fragmentation. Interestingly, community-level analysis revealed that predator functional richness was greatest in fragmented landscapes while response diversity for one functional group was low. From these results, I conclude that fragmented landscapes contained predator species with more diverse functional traits.

My overall results of community-level functional diversity are contrary to what I predicted. Previous studies at the species level found that predatory beetles are sensitive to habitat edges (Costa et al. 2013) and are in lower abundance in isolated stands relative to the abundance of their prey (Ryall & Fahrig 2005). Also, it has been previously observed that wood-borer abundance may be higher in herbaceous fringes rather than forests (Wermelinger et al. 2007). Although these studies investigate community change at the species level, my logic behind this prediction was based on two assumptions about functional diversity. First, a greater number of species would be more likely to share more diverse functional traits between them (Tilman et al. 1996). Also, at least regarding functional diversity in plant communities, Walker et al. (1999) found that dominant

species have more diverse trait profiles, and although the rare species also have diverse traits among them, they provide ecosystem resilience by having differing responses to disturbance. Therefore, applying this previous knowledge to possible changes at the functional diversity level in my community, I expected that predator functional diversity would be more negatively affected by fragmentation than wood-borer functional diversity. I propose that discrepancies resulting from my study measured at the functional group level and previous studies on wood-borers and predator beetles (measured at the species level) are due to the assessment of different levels of diversity (species vs. function).

Despite changes in functional diversity at the community level not meeting my predictions, I found that both wood-borer and predator functional groups generally had compromised resilience along the gradient. However, among the five functional groups, only functional group FG2 had all species missing at some of the sites. I propose that the resilience of this community was due to high functional redundancy within functional groups as well as the presence of two ecological stabilizing mechanisms, cross-scale resilience and response diversity.

I developed new methodology to detect cross-scale resilience that involved assessing species' response to the entire range of ecologically relevant analytical foci. I considered cross-scale resilience to be occurring in the community if ecosystem function was similarly dispersed among these variable species' response trends. I found not only that species could be grouped by their response to the landscape across all relevant foci, but that these trends were equally distributed among functional groups. This approach to detect cross-scale resilience was ecologically relevant because it aimed to determine how

species responded across the entire landscape relevant to their ecology and not just a single analytical focus.

Also, I assessed response diversity as both FDis (Chapter 3) and by directly determining whether species responded differently to the same disturbance (Chapter 4). Although FDis for three of five functional groups was reduced with fragmentation, I found that species in all functional groups (except FG2) responded differently to disturbance, thus the ecosystem stability mechanism "response diversity" was detected in this community. Interestingly, FG2 contained the fewest species among the functional groups, which I propose contributed to the loss of all species at some of the sites. Fewer species within the functional group means that the group has less functional redundancy which could lower its resilience to habitat change. The functional redundancy of this group was further reduced in fragmented landscapes. Furthermore, having few species in this group makes it more difficult to detect differing responses by species in this group in response to disturbance.

I also developed new methodology that used visual contrasts to link and examine predator and prey abundances in a multitrophic community. I found that prey visual contrasts moderated the degree to which the abundance of substrate-foraging birds with a violet-sensitive (VS) visual system impacted beetle abundance. Interestingly, the link's resolution was enhanced when I matched beetle and bird species that utilize similar forest habitat as part of their functional roles. I found support for my prediction that visual contrasts may not be as important for birds that flycatch, a hunting strategy that relies on detecting prey's movement from a distance. However, the photoreceptors (double cones) involved in detecting achromatic contrasts also detect movement, and I found a

significant relationship between beetles with low chromatic contrast but high achromatic contrast and flycatching birds. I did not find support for my prediction that visual contrasts moderate the degree to which the abundance of birds with an ultraviolet-sensitive (UVS) visual system impacts beetle abundance. Based on previous studies that demonstrate that UV signals influence avian predation differently, I propose that UV reflectance of a community of beetle prey has multiple roles in the signaling to a community of avian predators, thus resolution was lost in these comparisons.

I also found that beetle functional roles, as well as their visual contrasts, were important for linking trophic levels to compare predator and prey abundances. Insectivore birds are generalist predators that do not specialize on any particular insect species. They demonstrate prey switching behavior where birds feed on more abundant insects and then switch to feed on others that are high in abundance. Therefore I would not expect strong correlations between individual insect and bird species, which is consistent with what I observed for the majority of relationships. However, I observed strong correlations between beetle and bird species in tests where the abundance of visually apparant beetles to birds was compared to the abundance of birds that shared the same foraging habitat. Therefore, considering that I was able to observe these relationships by using a functional link, species' functional roles must also be an important component for detecting predator-prey interactions in communities.

My approach to examine species abundances between trophic levels is transferable to many other communities. Data on the visual systems of many other animals exist (and at least with birds, estimates on spectral tuning can be made). Furthermore, such studies can be implemented as long as equipment to measure

reflectance and irradiance is accessible. However, I suggest that future studies should strengthen the link between trophic levels by incorporating predator and prey functional roles.

Furthermore, my assessment of change in functional diversity was across a gradient of habitat fragmentation measured across analytical foci relevant to longhorned beetles and their beetle predators. This assessment was with models that included predictors consisting of landscape pattern measured at the most explanatory analytical focus. Analyses were conducted at the community and functional group levels. This approach allowed me to observe that functional diversity, like species, responds to the landscape at different landscape patterns measured at different foci (Figure 3.7, Appendix G, J, K) and also avoid a type 2 error. For instance, if functional diversity was assessed with a single predictor assessed at a single focus, I would have not detected many of the significant responses of functional diversity to landscape pattern.

Ultimately, if a functional group responds to disturbance at larger foci, it may be less perturbed by local disturbance and vice versa. This outcome of my research study demonstrates that ecologically relevant information may not be captured if functional diversity is assessed at a single focus. However, considering that ecological knowledge exists for species of interest, practices to promote functional diversity to preserve ecosystem function across local landscapes may be a realistic goal for the near future. My methods for producing three-dimensional curves of functional diversity at a community level may be one approach for these scenarios.

The results of this study further demonstrate that functional diversity is an appropriate measure for detecting change in multitrophic communities. For instance, I

found that a functional diversity approach was valuable for observing and identifying thresholds of community change, mechanisms that stabilize the communities from change, and observing the impact of predator-prey interactions on communities. Without this measure, the signal to detect these outcomes would have been muted. I suggest that future studies investigate how vision-mediated predator-prey interactions may simultaneously impact the functional diversity of these trophic levels.

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APPENDICES

Appendix A: Functional traits obtained for wood-boring beetles (Coleoptera: Cerambycidae)

Table A.1: Cerambycid functional traits subfamily, tribe, mean size, landscape response, avian visual perception

Species	Subfamily	Tribe	Mean Size (mm)	Landscape Response	Avian Visual Perception
Aegomorphus.modestus	Lam	Acad	13	LR.1	AV.5
Analeptura.lineola	Lep	Lept	10	LR.2	AV.4
Anelaphus.villosus	Cer	Elah	16	LR.3	AV.7
Astyleiopus.variegatus	Lam	Acan	8	LR.3	AV.7
Astylidius.parvus	Lam	Acan	5	LR.1	AV.8
Astylopsis.macula	Lam	Acan	8.5	LR.2	AV.8
Astylopsis.sexguttata	Lam	Acan	10	LR.3	AV.8
Bellamira.scalaris	Lep	Lept	26	LR.1	AV.4
Brachyleptura.champlaini	Lep	Lept	10	LR.1	AV.6
Callimoxys.s..sanguinicollis	Cer	Sten	10	LR.1	AV.2
Clytoleptus.albofasciatus	Cer	Clyt	8.5	LR.2	AV.3
Clytus.ruricola	Cer	Clyt	12.5	LR.3	AV.10
Cyrtophorus.verrucosus	Cer	Anag	9	LR.2	AV.2
Dorcaschema.cinereum	Lam	Dorc	10.5	LR.1	AV.3
Dorcashema.nigrum	Lam	Dorc	9.5	LR.1	AV.2
Eburia.quadrigeminata	Cer	Ebur	18.5	LR.1	AV.4
Ecyrus.d..dasycerus	Lam	Pogo	9	LR.1	AV.8
Elaphidion.mucronatum	Cer	Elap	19	LR.2	AV.7
Elytramatatrix.undata	Dis	Dist	20.5	LR.2	AV.8

Table A.1: Cerambycid functional traits subfamily, tribe, mean size, landscape response, avian visual perception, *continued*.

Enaphalodes.atomarius	Cer	Elap	25	LR.2	AV.7
Euderces.picipes	Cer	Till	7	LR.3	AV.3
Eupogonius.pauper	Lam	Desm	8.5	LR.2	AV.7
Eupogonius.pubescens	Lam	Desm	5	LR.3	AV.3
Eupogonius.subarmatus	Lam	Desm	7	LR.3	AV.2
Gaurotes.cyanipennis	Lep	Lept	11	LR.3	AV.5
Gracilia.minuta	Cer	Grac	4.9	LR.3	AV.6
Grammoptera.ruficeps	Lep	Lept	5.8	LR.1	AV.3
Graphisurus.despectus	Lam	Acan	11.5	LR.1	AV.8
Graphisurus.fasciatus	Lam	Acan	12	LR.2	AV.7
Heterachthes.quadrimaculatus	Cer	Ibid	10.5	LR.3	AV.4
Hyperplatys.aspersa	Lam	Acan	7	LR.1	AV.8
Hyperplatys.maculata	Lam	Acan	5.1	LR.2	AV.8
Leptostylus.transversus	Lam	Acan	10	LR.2	AV.8
Leptura.plebeja	Lep	Lept	12.2	LR.1	AV.2
Lepturges.angulatus	Lam	Acan	7	LR.1	AV.7
Lepturges.confluens	Lam	Acan	8.75	LR.3	AV.7
Lepturges.pictus	Lam	Acan	8.75	LR.3	AV.7
Lepturges.symmetricus	Lam	Acan	7.5	LR.1	AV.8
Megacyllene.caryae	Cer	Clyt	15	LR.2	AV.10
Metacmaeops.vittata	Lep	Lept	7	LR.2	AV.10
Microgoes.oculatus	Lam	Lami	10.2	LR.2	AV.8
Molorchus.b..bimaculatus	Cer	Molo	6.5	LR.3	AV.3
Neandra.brunnea	Par	Para	14	LR.2	AV.3
Necydalis.mellita	Lep	Necy	21.5	LR.1	AV.2

Table A.1: Cerambycid functional traits subfamily, tribe, mean size, landscape response, avian visual perception, *continued*.

Neoclytus.a..acuminatus	Cer	Clyt	8.5	LR.2	AV.9
Neoclytus.m..mucronatus	Cer	Clyt	14	LR.2	AV.10
Neoclytus.scutellaris	Cer	Clyt	12	LR.3	AV.10
Oberea.praelonga	Lam	Phyt	10	LR.1	AV.3
Obrium.rufulum	Cer	Obri	7	LR.1	AV.6
Orthosoma.brunneum	Pri	Prio	37.5	LR.3	AV.3
Parelaphidion.aspersum	Cer	Elap	16	LR.3	AV.7
Parelaphidion.incertum	Cer	Elap	16	LR.3	AV.7
Phymatodes.amoenus	Cer	Call	6	LR.1	AV.2
Phymatodes.lengi	Cer	Call	5	LR.1	AV.2
Phymatodes.testaceus	Cer	Call	12.5	LR.1	AV.2
Prionus.laticollis	Pri	Prio	36	LR.3	AV.2
Psenocerus.supernotatus	Lam	Desm	6.5	LR.1	AV.3
Saperda.discoidea	Lam	Sape	13	LR.1	AV.3
Saperda.imitans	Lam	Sape	13.5	LR.2	AV.9
Saperda.lateralis	Lam	Sape	11.5	LR.1	AV.4
Saperda.tridentata	Lam	Sape	16.5	LR.1	AV.9
Saperda.vestita	Lam	Sape	17	LR.1	AV.3
Sarosesthes.fulminans	Cer	Clyt	20	LR.2	AV.9
Sphenostethus.taslei	Pri	Sole	21	LR.1	AV.2
Stenelytrana.emarginata	Lep	Lept	31	LR.1	AV.6
Stenocorus.cinnamopterus	Lep	Lept	12	LR.3	AV.6
Stenocorus.schaumii	Lep	Lept	23	LR.1	AV.2
Sternidius.alpha	Lam	Acan	6.5	LR.2	AV.8

Table A.1: Cerambycid functional traits subfamily, tribe, mean size, landscape response, avian visual perception, *continued*.

Strangalepta.abbreviata	Lep	Lept	13	LR.2	AV.4
Strangalia.bicolor	Lep	Lept	14	LR.1	AV.2
Strangalia.luteicornis	Lep	Lept	11.5	LR.3	AV.10
Strangalia.solitaria	Lep	Lept	13.5	LR.1	AV.6
Strophiona.nitens	Lep	Lept	12.5	LR.1	AV.10
Tessaropa.tenuipes	Cer	Meth	8	LR.2	AV.2
Typocerus.acuticauda	Lep	Lept	14	LR.1	AV.6
Typocerus.deceptus	Lep	Lept	16	LR.1	AV.4
Typocerus.v..velutinus	Lep	Lept	12.5	LR.2	AV.10
Urgleptes.querci	Lam	Acan	5	LR.2	AV.3
Urgleptes.signatus	Lam	Acan	7	LR.3	AV.3
Xylotrechus.colonus	Cer	Clyt	11.5	LR.3	AV.4
Xylotrechus.convergens	Cer	Clyt	10.5	LR.3	AV.4

Table A.2: Abbreviations for Table 1 and literature cited for Tribe and Subfamily.

Tribe		**Subfamily**	
Acanthocinini	Acan	Cerambycinae	Cer
Acanthoderini	Acad	Disteniinae	Dis
Anaglyptini	Anag	Lamiinae	Lam
Callidiini	Call	Lepturninae	Lep
Clytini	Clyt	Parandrinae	Par
Desmiphorini	Desm	Prioninae	Pri
Disteniini	Dist		
Dorcaschematini	Dorc	**Landscape Response**	
Eburiini	Ebur	Linear	LR.1
Elaphidiini	Elah	Second order polynomial	LR.2
Elaphidioinini	Elap	Third order polynomial	LR.3
Graciliini	Grac		
Ibidionini	Ibid		
Lamiini	Lami		
Lepturini	Lept		
Methiini	Meth		
Molorchini	Molo		
Necydalini	Necy		
Obriini	Obri	**Literature Cited**	
Parandrini	Para	Abdel Moniem & Holland (2013)	
Phytoecini	Phyt	Arnett et al. (2002)	
Pogonocherini	Pogo	Gosling & Gosling (1977)	
Prionini	Prio	Knull (1946)	
Saperdini	Sape	Lingafelter (2007)	
Solenopterini	Sole	Linsley & Chemsak (1995)	
Stenopterini	Sten	Linsley & Chemsak (1984)	
Tillomorphini	Till	Yanega (1996)	

Table A.3: Cerambycid functional traits Hymenoptera resemblance, diel activity, host range, host genera, host family. Blank entries indicate missing values.

Species	Hymenoptera Resemblance	Diel Activity	Host Range	Host genera #	Host Family #
Aegomorphus.modestus	none	N, C	Poly	23	13
Analeptura.lineola	none		Poly	5	3
Anelaphus.villosus	none	N	Poly	28	16
Astyleiopus.variegatus	none	N, C	Poly	22	14
Astylidius.parvus	none	N, C	Poly	14	9
Astylopsis.macula	none	N, C	Poly	19	12
Astylopsis.sexguttata	none	N, C	Poly	5	3
Bellamira.scalaris	none	D	Poly	9	7
Brachyleptura.champlaini	none		Mono	1	1
Callimoxys.s..sanguinicollis	parasitoid	D	Poly	19	13
Clytoleptus.albofasciatus	ant	D	Poly	2	2
Clytus.ruricola	wasp	D	Poly	10	6
Cyrtophorus.verrucosus	ant		Poly	22	13
Dorcaschema.cinereum	none		Poly	9	7
Dorcashema.nigrum	none	N, C	Poly	2	2
Eburia.quadrigeminata	none		Poly	10	7
Ecyrus.d..dasycerus	none	N, C	Poly	17	12
Elaphidion.mucronatum	none	N, C	Poly	28	19
Elytramatatrix.undata	none	N	Poly	6	6
Enaphalodes.atomarius	none	N, C	Poly	7	5
Euderces.picipes	ant	D	Poly	19	10
Eupogonius.pauper	none	N, C	Poly	20	16

Table A.3: Cerambycid functional traits Hymenoptera resemblance, diel activity, host range, host genera, host family. Blank entries indicate missing values, *continued.*

Eupogonius.pubescens	none	N, C	Mono	1	1
Eupogonius.subarmatus	none		Poly	5	5
Gaurotes.cyanipennis	none	D	Poly	9	7
Gracilia.minuta	none		Poly	10	8
Grammoptera.ruficeps	none		Poly	8	6
Graphisurus.despectus	none		Mono	18	13
Graphisurus.fasciatus	none		Poly	18	13
Heterachthes.quadrimaculatus	none		Poly	4	4
Hyperplatys.aspersa	none	N, C	Poly	24	18
Hyperplatys.maculata	none	N, C	Poly	22	16
Leptostylus.transversus	none	N, C	Poly	29	21
Leptura.plebeja	none		Olig	2	1
Lepturges.angulatus	none	N, C	Poly	14	8
Lepturges.confluens	none	N, C	Poly	7	5
Lepturges.pictus	none	N, C	Poly	3	2
Lepturges.symmetricus	none	N, C	Poly	10	7
Megacyllene.caryae	wasp	D	Poly	13	7
Metacmaeops.vittata	none		Poly	5	4
Microgoes.oculatus	none	N, C	Poly	14	12
Molorchus.b..bimaculatus	parasitoid	D	Poly	19	13
Neandra.brunnea	none		Poly	18	12
Necydalis.mellita	parasitoid		Olig	3	2
Neoclytus.a..acuminatus	wasp	D	Poly	37	21

Table A.3: Cerambycid functional traits Hymenoptera resemblance, diel activity, host range, host genera, host family. Blank entries indicate missing values, *continued*.

Neoclytus.m..mucronatus	wasp	D	Poly	4	4
Neoclytus.scutellaris	wasp	D	Poly	4	4
Oberea.praelonga	parasitoid	D	Poly	7	5
Obrium.rufulum	none		Mono	3	3
Orthosoma.brunneum	none	N	Poly	10	5
Parelaphidion.aspersum	none		Poly	4	4
Parelaphidion.incertum	none		Poly	6	6
Phymatodes.amoenus	none	D	Mono	1	1
Phymatodes.lengi	none	D			
Phymatodes.testaceus	none	D	Poly	10	5
Prionus.laticollis	none		Poly	13	10
Psenocerus.supernotatus	ant		Poly	25	18
Saperda.discoidea	none	N	Poly	7	5
Saperda.imitans	none		Poly	5	5
Saperda.lateralis	none		Poly	14	12
Saperda.tridentata	none	N	Mono	1	1
Saperda.vestita	none		Poly	3	3
Sarosesthes.fulminans	none	D	Poly	4	3
Sphenostethus.taslei	none		Poly	4	2
Stenelytrana.emarginata	none		Poly	8	6
Stenocorus.cinnamopterus	none		Poly	3	3
Stenocorus.schaumii	none		Poly	5	5
Sternidius.alpha	none		Poly	19	12

Table A.3: Cerambycid functional traits Hymenoptera resemblance, diel activity, host range, host genera, host family. Blank entries indicate missing values, *continued*.

Strangalepta.abbreviata	none		Poly	11	6
Strangalia.bicolor	wasp	D	Poly	2	2
Strangalia.luteicornis	none	D	Poly	6	5
Strangalia.solitaria	none	D	Poly	2	2
Strophiona.nitens	wasp		Poly	6	3
Tessaropa.tenuipes	parasitoid		Poly	8	5
Typocerus.acuticauda	none				
Typocerus.deceptus	wasp				
Typocerus.v..velutinus	wasp		Poly	6	5
Urgleptes.querci	none	N, C	Poly	30	20
Urgleptes.signatus	none	N, C	Poly	13	10
Xylotrechus.colonus	wasp	D	Poly	14	10
Xylotrechus.convergens	wasp	D	Mono	1	1

Table A.4: Abbreviations for Table 3 and literature cited for Hymenoptera resemblance, diel activity, host family, and host genera.

Diel Activity	
Diurnal	D
Nocturnal	N
Crepuscular	C
Host Range	
Polyphagous (feeding >1 plant Family)	Poly
Oligophagous (feeding>1 genus within one plant Family	Olig
Monophagous (feeding on 1 genera	Mono
Literature Cited: diel activity	
Krinsky & Godwin (1996)	
Linsley (1961)	
Linsley (1959)	
Solomon (1995)	
Literature Cited: Hymenoptera resemblance	
Linsley (1959)	

Table A.4: Abbreviations for Table 3 and literature cited for Hymenoptera resemblance, diel activity, host family, and host genera, *continued*.

Literature cited: host Family, host genera	
Beutenmuller (1896)	Linsley (1963)
Blackman & Stage (1918)	Linsley (1964)
Campbell et al. (1989)	Linsley & Chemsak (1972)
Craighead (1950)	Linsley & Chemsak (1976)
Craighead (1923)	Linsley & Chemsak (1984)
Drooz (1985)	Linsley & Chemsak (1995)
Gosling (1986)	Linsley & Chemsak (1997)
Gosling & Gosling (1977)	MacRae & Rice (2007)
Hoffman (1942)	McMinn & Crossley (1996)
Johnson & Lyon (1988)	Solomon (1995)
Knull (1946)	Vlasak & Vlasakova (2002)
Lingafelter (2007)	Warriner et al. (2004)
Linsley (1962a and b)	Yanega (1996)

Table A.5: Cerambycid functional traits host condition, larval wood type, adult feeding behavior, plant part attacked (larvae).

Species	Host Condition	Larval Wood Type	Adult feeding behavior	Plant part attacked
Aegomorphus.modestus	Dec	H,S,C,He		
Analeptura.lineola	D, Dec	H,C,S	F	T
Anelaphus.villosus	L, W, Dy, D	H,S,He,V,C	Tw	Tw, Br
Astyleiopus.variegatus	D	H,S,V,He		Br
Astylidius.parvus		H,S,He,V		
Astylopsis.macula	L	H,S,He,V		Tw
Astylopsis.sexguttata	D	H,C,He		
Bellamira.scalaris	Dec	H,C	F	T
Brachyleptura.champlaini		C	F	
Callimoxys.s..sanguinicollis	D	H,S,V	F	Tw, Br
Clytoleptus.albofasciatus	D, Dy	H,V		T, Br
Clytus.ruricola	D, Dec	H,S	F	
Cyrtophorus.verrucosus	D	H,S,C	F	
Dorcaschema.cinereum	D	H,S	L	Tw, Br
Dorcashema.nigrum	Dy, D	H	L	Br
Eburia.quadrigeminata	L, D	H,S		T
Ecyrus.d..dasycerus	D	H,S,V		Tw, Br
Elaphidion.mucronatum	D	H,S,He,V		T, Br, Tw
Elytramatatrix.undata	D	H,C,S		R
Enaphalodes.atomarius	D	H,S		T
Euderces.picipes	D	H,S,He	F	Br
Eupogonius.pauper		H,S,V		

Table A.5: Cerambycid functional traits host condition, larval wood type, adult feeding behavior, plant part attacked (larvae), *continued*.

Eupogonius.pubescens	D	H		Br
Eupogonius.subarmatus	D	H,V	L	Br
Gaurotes.cyanipennis	Dy, D	H,S	F	
Gracilia.minuta	Dy, D	H,S		Tw, Br
Grammoptera.ruficeps		H,S,He	F	
Graphisurus.despectus	D	H,C,S, He	B	
Graphisurus.fasciatus	D	H,C,S,He	B	
Heterachthes.quadrimaculatus	D	H		Br
Hyperplatys.aspersa	D	H,S,V,He	Tw, Br	
Hyperplatys.maculata	D	H,S,V	B	Tw, Br
Leptostylus.transversus	D	H,C,S,V,He	B	
Leptura.plebeja		C	F	
Lepturges.angulatus	D	H,S,C		Br
Lepturges.confluens	D, Dec	H	B	T, Br
Lepturges.pictus	D	H		Br
Lepturges.symmetricus	D	H,S		Br
Megacyllene.caryae	D	H,S,V	F	T
Metacmaeops.vittata	Dec	H,C	F	
Microgoes.oculatus	D	H,S,C		
Molorchus.b..bimaculatus	D	H,S,V	F	Tw, Br
Neandra.brunnea	W, Dec	H,C		T
Necydalis.mellita	D	HC		
Neoclytus.a..acuminatus	L, W, Dy, D	H,S,C,V,He		T, Br

Table A.5: Cerambycid functional traits host condition, larval wood type, adult feeding behavior, plant part attacked (larvae), *continued*.

Neoclytus.m..mucronatus	D, Dy	H,C	F	T
Neoclytus.scutellaris	D	H,V		T, Br
Oberea.praelonga		H,S		
Obrium.rufulum	D, Dy	H		Br
Orthosoma.brunneum	Dec	H,C		
Parelaphidion.aspersum	D, Dec	H,S		T
Parelaphidion.incertum	L, Dy, D	H,S		T, Br
Phymatodes.amoenus	D	V		
Phymatodes.lengi				
Phymatodes.testaceus	D	H,C		T, Br
Prionus.laticollis	L	H,C,S	none	T, R
Psenocerus.supernotatus	D, Dy, Dec	H,S,V,He		T, Br
Saperda.discoidea	W, Dy, D	H,S	B	T
Saperda.imitans	D	H		
Saperda.lateralis	W, Dy, D	H,S,He	L	T
Saperda.tridentata	W, Dy, D	H	L, Tw	Br
Saperda.vestita	L, D	H	B, L	T, Br, R
Sarosesthes.fulminans	D	H,He		T
Sphenostethus.taslei	D	H		
Stenelytrana.emarginata	Dec	H	F	T, Br
Stenocorus.cinnamopterus		H,S	F	
Stenocorus.schaumii		H,S	F	
Sternidius.alpha	D	H,S,V	Br	Br, Tw

Table A.5: Cerambycid functional traits host condition, larval wood type, adult feeding behavior, plant part attacked (larvae), *continued*.

Strangalepta.abbreviata	Dec	H,C	F	
Strangalia.bicolor	Dec	H	F	
Strangalia.luteicornis	Dec	H,S,V	F	Br
Strangalia.solitaria		H		
Strophiona.nitens	L, D	H	F	T, Br
Tessaropa.tenuipes	D	H,S		Br, Tw
Typocerus.acuticauda			F	
Typocerus.deceptus			F	
Typocerus.v..velutinus	Dec	H,C	F	
Urgleptes.querci	D	H,C,S,V,He	Br	Br, Tw
Urgleptes.signatus	D	H,S	Br	Br
Xylotrechus.colonus	D, Dy	H,C		T, Br
Xylotrechus.convergens	D	H		Br

Table A.6: Abbreviations for Table5 and literature cited for host condition, larval wood type, adult feeding behavior, and plant part attacked (larvae).

Host Condition		**Literature Cited: host condition and larval wood type**
Dead	D	Beutenmuller (1896)
Decomposing	Dec	Blackman & Stage (1918)
Dying	Dy	Campbell et al. (1989)
Living	L	Craighead (1923)
Weakened	W	Craighead (1950)
		Drooz (1985)
Larval Wood Type		Gosling (1986)
Conifer	C	Gosling & Gosling (1977)
Hardwood	H	Hoffman (1942)
Herbacious	He	Johnson & Lyon (1988)
Shrub	S	Knull (1946)
Vine	V	Lingafelter (2007)
		Linsley (1962a and b)
Feeding		Linsley (1963)
Bark	B	Linsley (1964)
Branches	Br	Linsley & Chemsak (1976)
Cambium	C	Linsley & Chemsak (1972)
Flowers	F	Linsley & Chemsak (1984)
Foliage	L	Linsley & Chemsak (1995)
Heartwood	H	Linsley & Chemsak (1997)
Roots	R	MacRae & Rice (2007)
Sapwood	S	McMinn & Crossley (1996)
Trunk	T	Solomon (1995)
Twigs	Tw	Vlasak & Vlasakova (2002)
		Warriner et al. (2004)
		Yanega (1996)

Table A.6: Abbreviations for Table 5 and literature cited for host condition, larval wood type, adult feeding behavior, and plant part attacked (larvae), *continued*.

Literature cited: adult feeding behavior, plant part attacked, plant layer attacked

Berlocher et al. (1992)
Beutenmuller (1896)
Blackman & Stage (1918)
Campbell et al. (1989)
Craighead (1923)
Craighead (1950)
Drooz (1985)
Felt & Joutel (1904)
Gosling (1986)
Gosling & Gosling (1977)
Hoffman (1942)
Holland, J. D., personal observation
Johnson & Lyon (1988)
Knull (1946)
Lingafelter (2007)
Linsley (1962a and b)
Linsley (1963)
Linsley (1964)
Linsley & Chemsak (1972)
Linsley & Chemsak (1976)
Linsley & Chemsak (1984)
Linsley & Chemsak (1995)
Linsley & Chemsak (1997)
MacRae & Rice (2007)
McDowel (2011)
McMinn & & Crossley (1996)
Shour (2015)
Solomon (1995)
Warriner et al. (2002)
Yanega (1996)

*Habits of *Callimoxys s. sanguinicollis* are similar to *Molorchus b. bimaculatus* (Craighead 1923), so I combined the feeding habits of these two species in the trait table.

Table A.7: Cerambycid functional traits, plant layer attacked (larvae), flight period.

Species	Plant layer attacked	Flight Period
Aegomorphus.modestus		May-Sep
Analeptura.lineola		May-Aug
Anelaphus.villosus	C, S	Apr-Sep
Astyleiopus.variegatus		Jun-Sep
Astylidius.parvus		May-Aug
Astylopsis.macula	B, C	May-Sep
Astylopsis.sexguttata	C	Apr-Sep
Bellamira.scalaris	C	May-Aug
Brachyleptura.champlaini		Jun-Aug
Callimoxys.s..sanguinicollis	C, S	Jun-Jul
Clytoleptus.albofasciatus		May-Aug
Clytus.ruricola		May-Jul
Cyrtophorus.verrucosus	S	Apr-Jul
Dorcaschema.cinereum	C, S	May-Jul
Dorcashema.nigrum	S	May-Aug
Eburia.quadrigeminata	H	Jun-Jul
Ecyrus.d..dasycerus		Mar-May
Elaphidion.mucronatum	C, S	May-Jul
Elytramatatrix.undata	S	Jun-Sep
Enaphalodes.atomarius	C, S	May-Sep
Euderces.picipes	C	May-Jul
Eupogonius.pauper		Mar-Nov
Eupogonius.pubescens		Jun-Jul
Eupogonius.subarmatus		May-Aug
Gaurotes.cyanipennis	C	May-Aug
Gracilia.minuta	C	May-Jul
Grammoptera.ruficeps		Apr-Jul
Graphisurus.despectus	C	May-Jul
Graphisurus.fasciatus	C	Apr-Oct
Heterachthes.quadrimaculatus		May-Aug
Hyperplatys.aspersa	C, S	Mar-Sep
Hyperplatys.maculata		May-Oct
Leptostylus.transversus		Mar-Oct

Table A.7: Cerambycid functional traits, plant layer attacked (larvae), flight period, *continued*.

Leptura.plebeja		Jun-Aug
Lepturges.angulatus		Mar-Aug
Lepturges.confluens		May-Aug
Lepturges.pictus		May-Jul
Lepturges.symmetricus		May-Aug
Megacyllene.caryae	C, S, H	May-Jun
Metacmaeops.vittata		Jun-Jul
Microgoes.oculatus	C	Jun-Aug
Molorchus.b..bimaculatus	C, S	Apr-Jul
Neandra.brunnea	S, H	Mar-Nov
Necydalis.mellita	H	May-Aug
Neoclytus.a..acuminatus	C, S	May-Aug
Neoclytus.m..mucronatus	C	Jun-Jul
Neoclytus.scutellaris	S	Jun-Aug
Oberea.praelonga		May-Jul
Obrium.rufulum		Jun-Jul
Orthosoma.brunneum	H	Jul-Sep
Parelaphidion.aspersum	B	Jun-Oct
Parelaphidion.incertum	B, C	Apr-Sep
Phymatodes.amoenus	S	Apr-Aug
Phymatodes.lengi		Jun
Phymatodes.testaceus	C	May-Jun
Prionus.laticollis	B, C	Jul, Aug
Psenocerus.supernotatus	C, S, H	Apr-Jul
Saperda.discoidea	C, S	May-Sep
Saperda.imitans		May-Jul
Saperda.lateralis	C	May-Aug
Saperda.tridentata	B, C, S	Apr-Aug
Saperda.vestita	C	May-Sep
Sarosesthes.fulminans	C, S	May-Aug
Sphenostethus.taslei		Jun-Aug
Stenelytrana.emarginata		Apr-Aug
Stenocorus.cinnamopterus		Apr-Jul
Stenocorus.schaumii		May-Jul
Sternidius.alpha		May, Jul

Table A.7: Cerambycid functional traits, plant layer attacked (larvae), flight period, *continued*.

Strangalepta.abbreviata		May-Aug
Strangalia.bicolor		Jun-Jul
Strangalia.luteicornis		May-Aug
Strangalia.solitaria		May-Sep
Strophiona.nitens	B, C, S	Mun-Jul
Tessaropa.tenuipes		Apr-May
Typocerus.acuticauda		Jun-Aug
Typocerus.deceptus		Jun-Jul
Typocerus.v..velutinus		May-Aug
Urgleptes.querci	S	May-Sep
Urgleptes.signatus		Jun-Aug
Xylotrechus.colonus	B, C	June
Xylotrechus.convergens	H	June

Table A.8: Abbreviations for Table 7 and literature cited for flight period.

Feeding		**Literature cited: flight period**
Bark	B	Lingafelter (2007)
Branches	Br	Linsley (1962a and b)
Cambium	C	Linsley (1963)
Flowers	F	Linsley (1964)
Foliage	L	Linsley & Chemsak (1972)
Heartwood	H	Linsley & Chemsak (1976)
Roots	R	Linsley & Chemsak (1984)
Sapwood	S	Linsley & Chemsak (1995)
Trunk	T	Solomon (1995)
Twigs	Tw	Waters & Hyche (1984)
		Yanega (1996)

Table A.9: Cerambycid functional traits, host family.

Species	Host Family
Aegomorphus.modestus	Ace, Bet, Cor, Fab, Fag, Jug, Mag, Ole, Pin, Ros, Sal, Til, Ulm
Analeptura.lineola	Bet, Fag, Pin
Anelaphus.villosus	Ace, Ana, Bet, Cel, Fab, Fag, Ham, Jug, Lau, Mor, Pin, Ros, Rut, Til, Ulm, Vit
Astyleiopus.variegatus	Ace, Ana, Cel, Eri, Fab, Fag, Hip, Jug, Mor, Rut, Sal, Ulm, Vis, Vit
Astylidius.parvus	Ace, Ana, Cel, Ebe, Fab, Hip, Mor, Rut, Ulm
Astylopsis.macula	Ace, Ana, Bet, Cel, Cor, Fag, Ham, Hip, Jug, Ros, Til, Ulm
Astylopsis.sexguttata	Ana, Mag, Pin
Bellamira.scalaris	Ace, Bet, Fag, Jug, Mag, Pin, Sal
Brachyleptura.champlaini	Pin
Callimoxys.s..sanguinicollis	Ace, Ana, Bet, Cor, Fab, Fag, Ham, Jug, Ole, Rha, Ros, Ulm, Vit
Clytoleptus.albofasciatus	Jug, Vit
Clytus.ruricola	Ace, Bet, Fag, Jug, Ros, Til
Cyrtophorus.verrucosus	Ace, Bet, Cor, Ebe, Fab, Fag, Jug, Lau, Mag, Pin, Ros, Til, Ulm
Dorcaschema.cinereum	Ace, Cor, Hip, Jug, Mor, Til, Ulm
Dorcashema.nigrum	Hip, Jug
Eburia.quadrigeminata	Ace, Fab, Fag, Jug, Ole, Ros, Ulm
Ecyrus.d..dasycerus	Ace, Fab, Fag, Jug, Mag, Mor, Ros, Sal, Scr, Til, Ulm, Vit
Elaphidion.mucronatum	Ace, Ana, Ann, Are, Bet, Cor, Cup, Ebe, Fab, Fag, Jug, Lau, Mag, Mor, Myr, Ros, Sal, Ulm, Vit
Elytramatatrix.undata	Bet, Fab, Fag, Jug, Pin, Ulm
Enaphalodes.atomarius	Ace, Fag, Jug, Ros, Ulm

Table A.9: Cerambycid functional traits, host family, *continued*.

Euderces.picipes	Ace, Ana, Bet, Cor, Fab, Fag, Jug, Ros, Sal, Ulm
Eupogonius.pauper	Ace, Ana, Ann, Bet, Cel, Cor, Fab, Fag, Ham, Jug, Mor, Ole, Ros, Rut, Til, Ulm
Eupogonius.pubescens	Til
Eupogonius.subarmatus	Cel, Fag, Ros, Til, Ulm
Gaurotes.cyanipennis	Ana, Bet, Cor, Fag, Jug, Mor, Ros
Gracilia.minuta	Bet, Fab, Fag, Hip, Rha, Ros, Rut, Sal
Grammoptera.ruficeps	Bet, Cap, Cor, Fag, Rha, Ros
Graphisurus.despectus	Ace, Ana, Bet, Cor, Fag, Ham, Jug, Mag, Ole, Pin, Ros, Til, Ulm
Graphisurus.fasciatus	Ace, Ana, Bet, Cor, Fag, Ham, Jug, Mag, Ole, Pin, Ros, Til, Ulm
Heterachthes.quadrimaculatus	Bet, Fag, Jug, Mag
Hyperplatys.aspersa	Ace, Ana, Ast, Bet, Cel, Cor, Fab, Fag, Gro, Jug, Lau, Mag, Men, Ole, Ros, Sal, Til, Ulm
Hyperplatys.maculata	Ace, Ana, Bet, Cor, Fab, Fag, Gro, Hip, Jug, Mag, Men, Ros, Rut, Sal, Til, Ulm
Leptostylus.transversus	Ace, Ana, Bet, Bur, Cor, Cup, Ebe, Fab, Fag, Ham, Hip, Jug, Mag, Mor, Pin, Pla, Rhi, Ros, Rut, Til, Ulm
Leptura.plebeja	Pin
Lepturges.angulatus	Fab, Fag, Hip, Jug, Mor, Pin, Ros, Ulm
Lepturges.confluens	Cor, Ebe, Fag, Ham, Jug
Lepturges.pictus	Jug, Ulm
Lepturges.symmetricus	Ace, Cor, Fag, Jug, Mor, Til, Ulm
Megacyllene.caryae	Fab, Fag, Jug, Mor, Ole, Ulm, Vit
Metacmaeops.vittata	Cup, Fag, Mag, Pin
Microgoes.oculatus	Ace, Ana, Bet, Cor, Eri, Fab, Fag, Jug, Ole, Pin, Sal, Til
Molorchus.b..bimaculatus	Ace, Ana, Bet, Cor, Fab, Fag, Ham, Jug, Ole, Rha, Ros, Ulm, Vit

Table A.9: Cerambycid functional traits, host family, *continued*.

Neandra.brunnea	Ace, Fab, Fag, Ham, Jug, Mag, Pin, Ros, Sal, Scr, Til, Ulm
Necydalis.mellita	Fag, Pin
Neoclytus.a..acuminatus	Ace, Aqu, Ana, Bet, Cap, Cor, Cup, Ebe, Fab, Fag, Ham, Jug, Lau, Mag, Mor, Ole, Ros, Sal, Til, Ulm, Vit
Neoclytus.m..mucronatus	Ebe, Jug, Pin, Ulm
Neoclytus.scutellaris	Fag, Jug, Ulm, Vit
Oberea.praelonga	Bet, Cap, Cor, Ros, Ulm
Obrium.rufulum	Fag, Ole, Til
Orthosoma.brunneum	Ace, Fag, Jug, Pin, Til
Parelaphidion.aspersum	Bet, Fag, Jug, Ulm
Parelaphidion.incertum	Ast, Fab, Fag, Jug, Mor, Ulm
Phymatodes.amoenus	Vit
Phymatodes.lengi	Vit*
Phymatodes.testaceus	Fag, Jug, Pin, Ros, Sal
Prionus.laticollis	Ace, Cor, Eri, Fag, Jug, Pin, Ros, Sal, Til, Vit
Psenocerus.supernotatus	Ace, Ana, Ast, Big, Cap, Cel, Cor, Fag, Gro, Ham, Jug, Lau, Mag, Men, Ros, Sal, Ulm, Vit
Saperda.discoidea	Car, Jug, Ros, Sal, Ulm
Saperda.imitans	Ace, Jug, Ros, Sal, Til
Saperda.lateralis	Ace, Ana, Bet, Cap, Fag, Ham, Jug, Ole, Pin, Ros, Til, Ulm
Saperda.tridentata	Ulm
Saperda.vestita	Ace, Sal, Til
Sarosesthes.fulminans	Api, Fag, Jug
Sphenostethus.taslei	Fab, Fag

Table A.9: Cerambycid functional traits, host family, *continued*.

Stenelytrana.emarginata	Ace, Bet, Cor, Fag, Mag, Ulm
Stenocorus.cinnamopterus	Cel, Hyd, Ros
Stenocorus.schaumii	Ace, Fag, Jug, Ole, Ros
Sternidius.alpha	Ace, Ana, Bet, Ebe, Fab, Fag, Jug, Mor, Pla, Ros, Rut, Ulm
Strangalepta.abbreviata	Ace, Bet, Cup, Fag, Pin, Sal
Strangalia.bicolor	Ace, Fag
Strangalia.luteicornis	Bet, Cap, Fag, Ulm, Vit
Strangalia.solitaria	Bet, Fag,
Strophiona.nitens	Ace, Fag, Jug
Tessaropa.tenuipes	Bet, Fab, Fag, Jug, Ros
Typocerus.acuticauda	Bet, Fag, Jug, Pin, Sal*
Typocerus.deceptus	Bet, Fag, Jug, Pin, Sal*
Typocerus.v..velutinus	Bet, Fag, Jug, Pin, Sal
Urgleptes.querci	Ace, Ana, Ann, Bet, Cap, Cel, Cor, Eri, Fab, Fag, Hip, Jug, Mag, Mor, Ole, Pin, Ros, Sal, Til, Ulm
Urgleptes.signatus	Ace, Ana, Bet, Cor, Fab, Fag, Jug, Mor, Ole, Til
Xylotrechus.colonus	Ace, Bet, Cor, Fag, Jug, Ole, Pin, Ros, Sal, Ulm
Xylotrechus.convergens	Ros

Table A.10: Abbreviations for Table 9, literature cited for host family.

Host Family					
Aceracea	Ace	Ebenaceae	Ebe	Oleaceae	Ole
Aquifoliaceae	Aqu	Ericaceae	Eri	Pinaceae	Pin
Anacardiaceae	Ana	Fabaceae	Fab	Platanaceae	Pla
Annonaceae	Ann	Fagaceae	Fag	Rhamnaceae	Rha
Apiaceae	Api	Grossulariaceae	Gro	Rhizophoraceae	Rhi
Areaceae	Are	Hammamelidaceae	Ham	Rosaceae	Ros
Asteraceae	Ast	Hipppocastanaceae	Hip	Rutaceae	Rut
Betulaceae	Bet	Hydrangeaceae	Hyd	Salicaceae	Sal
Bignoniacea	Big	Juglandaceae	Jug	Scrophulariaceae	Scr
Burseracea	Bur	Lauraceae	Lau	Tiliaceae	Til
Caprifoliaceae	Cap	Magnoliaceae	Mag	Ulmaceae	Ulm
Caryocaraceae	Car	Menispermaceae	Men	Viscaceae	Vis
Celastraceae	Cel	Moraceae	Mor	Vitaceae	Vit
Cupressaceae	Cup	Myricaceae	Myr		

Literature Cited		
Beutenmuller (1896)	Lingafelter (2007)	Linsley & Chemsak (1995)
Blackman & Stage (1918)	Linsley (1963)	Linsley & Chemsak (1976)
Gosling (1986)	Linsley (1962a and b)	MacRae & Rice (2007)
Johnson & Lyon (1988)	Linsley & Chemsak (1997)	Vlasak & Vlasakova (2002)
		Yanega (1996)

*Habits of *Callimoxys s. sanguinicollis* are similar to *Molorchus b. bimaculatus* (Craighead 1923), so I combined the feeding habits of these two species in the trait table.

*I assumed that *Typocerus acuticauda* and *T. despectus* utilize similar host plant families to *T. velutinus*, and that *Phymatodes amoenus* utilize similar host plant families as *P. lengi* based on species' phylogenetic signal (Raje 2012).

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Appendix B: Functional traits obtained for predator beetles (Coleoptera: Cleridae, Cucujidae, Histeridae, Passandridae) and literature cited for wood-borer and predator functional traits

Table B.1: Predator functional traits, subfamily, mean size (mm), body form, resemblance, and avian visual perception.

Species	Subfamily	Mean Size (mm)	Body Form	Resemblance	Avian Visual Perception
Catogenus rufus	SF.Pas	8.50	D	none	AV.6
Chariessa pilosa	Char	10.25	ES	L, C	AV2
Cregya mixta	Creg	4.25	SR	none	AV4
Cregya oculata	Creg	5.25	SR	none	AV4
Cucujus clavipes	SF.Cuc	12.00	D	none	AV6
Cymatodera bicolor	Cyma	7.75	C	L	AV1
Cymatodera inornata	Cyma	9.00	C	none	AV5
Enoclerus nigripes	Enoc	6.00	EN	F	AV10
Hololepta aequalis	Holo	9.00	D	none	AV1
Hololepta lucida	Holo	7.50	D	none	AV1
Madoniella dislocatus	Mado	4.75	SR	none	AV10
Neorthopleura thoracica	Neor	7.50	C	none	AV2

Table B.1: Predator functional traits, subfamily, mean size (mm), body form, resemblance, and avian visual perception, *continued*.

Paromalus bistritatus	Paro	2.20	O	none	AV1
Paromalus seeversi	Paro	1.65	O	none	AV2
Paromalus seminulum	Paro	2.00	O	none	AV1
Placopterus thoracicus	Plac	6.50	EN	L, C	AV2
Platylomalus aequalis	Plat	3.15	D	none	AV1
Platysoma aurelianum	Plat	3.25	D	none	AV5
Platysoma gracile	Plat	2.75	C	none	AV1
Platysoma leconti	Plat	3.15	D	none	AV1
Priocera castanea	Prio	8.25	EN	none	AV2
Pyticeroides laticornis	Pyti	5.50	LR	none	AV2
Teretrius americanus	Tere	2.10	SC	none	AV2
Zenodosus sanguineus	Zeno	5.50	EN	none	AV5

Table B.2: Abbreviations for Table 1, literature cited for Subfamily, body form, and resemblance.

Subfamily		**Body Form**	
Abrainae	Abra	Cylindrical	C
Clerinae	Cler	Dorsoventrally flattened	D
Cucujidae subfamily	SF.Cuc	Elongate, stout	ES
Dendrophilinae	Dend	Long-rectangulate	LR
Enopliinae	Enop	Narrow, elongate	NE
Epiphloeinae	Epip	Oval	O
Histerinae	Hist	Short, rectangulate	SR
Passandridae subfamily	SF.Pas	Subcylindrical	SC
Thaneroclerinae	Than		
Tillinae	Till	**Literature Cited**	
		Bousquet & Laplante (2006)	
		Downie & Arnett (1996a and b)	
Resemblance			
Cantheridae	C	Evans (2014)	
Formicidae	F	Horn (1873)	
Lamperidae	L	Mawdsley (1994)	
		Wenzel (1936)	

Table B.3: Predator functional traits landscape response, diel activity, flight activity, tree type, and tree state.

Species	Landscape Response	Diel Activity	Flight Activity	Tree type	Tree State
Catogenus rufus	LR3		Mar-Sep	H, C	D, Dy
Chariessa pilosa	LR1	D	Apr-Sep	H, C, V	D, Dy
Cregya mixta	LR3		July-Aug		D
Cregya oculata	LR3		Mar-Sep	H, C, S, V	D
Cucujus clavipes	LR1		Mar-Jul	H, C	Dy, D, Dec
Cymatodera bicolor	LR2	N	Apr-Aug	H, C, S	D
Cymatodera inornata	LR2	N	May-Aug	H, C, S	D
Enoclerus nigripes	LR3		Mar-Sep	H, C	D, Dy
Hololepta aequalis	LR1	D	Apr-Sep	H, C	D
Hololepta lucida	LR1	D	Apr-Aug	H	D
Madoniella dislocatus	LR3	D	Apr-Sep	H, C, S	Dy, D
Neorthopleura thoracica	LR3	N	Apr-Aug	H, V	Dy, D

Table B.3: Predator functional traits landscape response, diel activity, flight activity, tree type, and tree state, *continued*.

Paromalus bistritatus	LR2	D	Mar-Sep	H	D, Dec
Paromalus seeversi	LR3	D	Aug	H	D, Dec
Paromalus seminulum	LR1	D	Mar-Sep	H	D
Placopterus thoracicus	LR3		Apr-Aug	H, S	Dy, D
Platylomalus aequalis	LR3	D	Apr-Aug	H	D
Platysoma aurelianum	LR2	D	May-Oct	H	D
Platysoma gracile	LR2	D	May-Sep	H, C	D
Platysoma leconti	LR2	D	Apr-Oct	H, C	D
Priocera castanea	LR2	N	Mar-Sep	H, C	Dy, D
Pyticeroides laticornis	LR1	D	May-Aug	H, C	Dy, D
Teretrius americanus	LR2	D	May-Aug	H, C	D
Zenodosus sanguineus	LR2	D, N	Apr-Sep	H, C	Dy, D

Table B.4: Abbreviations for Table 3, literature cited for diel activity, flight activity, tree type, and tree state.

Tree Type		**Literature Cited**
Hardwood	H	Bousquet & Laplante (2006)
Conifer	C	Böving & Champlain (1920)
Shrub	S	De Leon (1934)
Vine	V	Dimmock (1882)
		Downie & Arnett (1996a and b)
Tree State		Drooz (1985)
Dying	Dy	Evans (2014)
Dead	Dy	Gosling (1980)
Decaying	Dec	Leavengood (2008)
		Opitz (2007)
		Purdue Entomological Research
Diel Activity		Collection
Diurnal	D	Smith & Sears (1982)
Nocturnal	N	Wenzel (1936), Yelamos (2002)

Table B.5: Predator functional traits larval feeding, larval habitat, adult feeding, and adult habitat.

Species	Larval Feeding	Larval Habitat	Adult Feeding	Adult Habitat
Catogenus rufus	Ecto	G		B
Chariessa pilosa	L	G	L, A	B, L
Cregya mixta		B, G		B, G, Br
Cregya oculata		B, G	L	B, G, Br
Cucujus clavipes		B		B
Cymatodera bicolor	L, P	G	E, L, P	B, Br
Cymatodera inornata	L, P	G	E, L, P	B
Enoclerus nigripes		G	L, P, A	B, G, Br
Hololepta aequalis	E, L	B	E, L	B
Hololepta lucida	E, L	B	E, L	B
Madoniella dislocatus	E, L, P	G	E, L, P, A	B, G, Br, T
Neorthopleura thoracica		G		B, G, Br

Table B.5: Predator functional traits larval feeding, larval habitat, adult feeding, and adult habitat, *continued*.

Paromalus bistritatus	E, L	B	E, L	B, G
Paromalus seeversi	E, L	B	E, L	B, G
Paromalus seminulum	E, L	B	E, L	B, G
Placopterus thoracicus		G		B, G, Br, T, F
Platylomalus aequalis	E, L	B	E, L	B
Platysoma aurelianum	E, L	B	E, L	B
Platysoma gracile	E, L	G	E, L	B, G
Platysoma leconti	E, L	B	E, L	B, G
Priocera castanea		G	A	B, G, L, Br
Pyticeroides laticornis	E, L, A	G	E, L, A	B, Br, T
Teretrius americanus	E, L	G	L	G
Zenodosus sanguineus	E, L, P	G	E, L, P, A	B, L

Table B.6: Abbreviations for Table 3, literature cited for larval feeding, larval habitat, adult feeding, and adult habitat.

Larval and Adult Habitat		**Literature Cited**
Under bark	B	Baker (1972)
Galleries	G	Böving & Champlain (1920)
Logs (surface)	L	Dimmock (1882)
Branches	Br	Downie & Arnett (1996a and b)
Twigs	T	Drooz (1985)
Flowers	F	Evans (2014)
		Leavengood (2008)
Adult Feeding		Optiz (2007)
Eggs	E	Yelamos (2002)
Larvae	L	
Pupae	P	
Adults	A	
Larval Feeding		
Ectoparasite	Ecto	
Eggs	E	
Larvae	L	
Pupae	P	
Adults	A	

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Appendix C: Landscape metrics calculated at each of the 12 analytical foci (90 m – 7.29 km)

Aggregation index*
Edge density*
Effective mesh size
Forest density
Landscape division index*
Landscape shape index*
Largest patch index
Maximum fractal dimension index
Maximum patch area
Maximum patch core area
Maximum perimeter-area ratio*
Maximum shape index
Mean fractal dimension index*
Mean patch area*
Mean patch core area
Mean perimeter area ratio*
Mean shape index*
Minimum fractal dimension index
Minimum patch area
Minimum perimeter-area ratio
Minimum shape index*
Number of patches
Patch density*
Perimeter area fractal dimension index*
Proportion of landscape*
Proportion of landscape core
Proportion like adjacencies
Splitting index*
Total area*
Total core area
Total edge*

*Indicates landscape metrics selected for RDA, multiple regression, and model selection for threshold vs. linear response at each analytical focus

Table C.1: Radius of each analytical focus. Radii retained in analysis are highlighted in gray.

Analytical focus	Focus radius, km
1	0.09
2	0.15
3	0.27
4	0.45
5	0.63
6	0.81
7	1.35
8	1.89
9	2.43
10	4.05
11	5.67
12	7.29

Appendix D: Methods to assess the avian visual perception functional trait

I selected insect specimens from the reference collection in the laboratory and the Purdue Entomological Research Collection (PERC). The most recently curated specimens within species were used. Where sexual dimorphism was present within a beetle species, I chose only female beetle specimens. Many species of beetles in my dataset resemble Hymenoptera (Linsley 1959, Mawdsley 1994). Therefore, I included wasp species common to Indiana forests to compare beetles to these proposed mimicry models in avian tetrachromatic color space (Appendix E). For eusocial hymenoptera species, I preferred worker castes because they are more likely to be encountered by avian predators. I collected digital images of the dorsal surfaces of beetles and wasps with a LeicaM165 C microscope and LAS V4 version 4.2 software for image stacking. I assessed dorsal patterns in ImageJ (Schneider et al. 2012) by quantifying the percent area of each color in the pattern. I also categorized beetle color pattern (solid, striped, spotted, mottled, and uniform metallic).

To construct visual contrasts, I obtained reflectance spectra (beetles, wasps, and common visual backgrounds) using a StellarNet Black Comet C-50 portable spectroradiometer (StellarNet-Inc., Tampa, FL). I recorded measurements at 0.5 nm intervals from 300 to 700 nm using a micron fiber optic probe and a combination Tungsten Krypton and Xenon light source. I measured beetles and wasps in a small dark chamber. The probe was held at a constant 45º angle with the light shining in the direction of the insect's dorsal surface from a distance of 4 mm. For all species, reflectance spectra from four representative individuals were recorded using an

integration time of 300 ms and averaging every 3 scans. As specimen size permitted, I took three measurements from various regions of the insect body including the head, pronotum, and elytra for beetles and the pronotum and gaster for wasps.

I collected representative samples of visual backgrounds from the Ross Biological Reserve in Tippecanoe County, IN, USA (40.41°N, 87.07°W, WGS84) and included tree bark, moss, lichen, leaves and flowers of various species common to Indiana forests (Appendix E). These backgrounds were selected because they 1) are frequent foraging sites for birds (Jackson 1979) and 2) are common substrates within the habitat of the cerambycids (Linsley 1961) and the beetles that are their predators (Böving and Champlain 1920, Ulyshen et al. 2004) in my dataset. I made ten measurements of each background type including dorsal and posterior surfaces of leaves and flowers with the probe at a constant 45º to the object. Measurements were made with an integration time of 1000 ms and averaging every 10 scans. I averaged spectra across plant part (dorsal and ventral surfaces of leaves and flower petals, sepals, bark, lichen, and moss) measured at each wavelength to yield one average spectrum per background plant part.

Before averaging spectra from insects or backgrounds, I manually smoothed curves to remove the peak artifact at 650 – 655 nm produced by the deuterium lamp as part of the spectroradiometer apparatus. At each wavelength I averaged spectra across body region to yield one average spectrum per species. I then calculated a percent reflectance spectrum for each average spectrum. For insect species large enough for multiple regions to be measured, I weighted percent reflectances from each body region based on the percent area of that region made of the entire insect body obtained with ImageJ. I took white and dark references before measuring each species and background.

The white standard had reflectivity > 98%. I measured the dark reference by placing the probe against the white standard with no light source.

The visibility of color patterns in relation to backgrounds may differ under different environmental light conditions (Endler 1987, Endler 1993, Fernández-Juricic et al. 2012). Therefore, ambient light was measured among sites selected to represent a spectrum of forest light conditions: closed canopy, small gap, large gap, shelterwood, and clear cut (for details, Moore et al. 2012). The irradiance data were collected on August 25, 2014 at some of the beetle collection sites within the Morgan-Monroe State Forest, Indiana with a JAZ-ULM-200 irradiance module and an Ocean Optics Jaz Spectrometer. Data acquisition was restricted to 9:00 – 11:00 AM on a day with no cloud cover, conditions favoring the foraging of diurnal, insectivorous birds.

I used the percent reflectance and irradiance data in the R package pavo (Maia et al. 2013, R Core Team 2014) to construct chromatic and achromatic contrasts between 1) beetle species and wasp species and 2) between beetle species and backgrounds. Contrasts were made considering the five light conditions with two average bird models included in the package (modeling ultraviolet-sensitive (UVS) and violet-sensitive (VS) vision, respectively). I used these two models because avian species have visual sensitivity to the ultraviolet (approximately 355 – 400nm) or violet (approximately 400 – 426 nm) spectrum (Hart 2001). I also used pavo to obtain 20 colorimetric variables from the average spectra of each beetle and wasp species (Appendix F). For wood-boring beetles, predator beetles, and wasps, I conducted principal components analysis on 1) a matrix containing colorimetric variables and 2) a matrix containing all chromatic and achromatic contrasts. The number of principal components retained was determined with

a broken stick model (Legendre & Legendre 1998, p. 410). I loaded the first three PC axes (λ = 76.29 % for colorimetric) and the first four PC axes (λ = 96.06% for chromatic and achromatic contrasts) into an additional matrix containing the ImageJ analysis on beetle dorsal patterns and categorical variables describing insect dorsal patterns. I grouped traits into categories (e.g., four variables for color pattern) and weighted such that the total weight across traits within a category equaled 1. I computed Gower dissimilarity with this matrix, and I used Ward's clustering to group wood-borers and predators into categories of similar appearing species (from a bird's perspective), hereafter called categories of avian visual perception (#3 in Fig. 3.4). I then added these categories as a single trait into the functional groupings analysis.

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Appendix E: Backgrounds used in chromatic and achromatic contrasts for avian visual perception functional trait categorization

Table E.1: Hymenoptera species whose reflectance was measured for the avian visual perception functional trait categorization.

Hymentopera	Region
Ancistrocerus adiabatus (de Saussure)	gaster and pronotum for all specimens
Bembix americana Fabricius	
Camponotus chromaiodes Bolton	
Campsomeris plumipes (Drury)	
1 morphospecies of *Dasymutilla* spp. Ashmead	
Dolichovespula arenaria (Fabricius)	
Euodynerus foraminatus (de Saussure)	
Formica exsectoides Forel	
Polistes metricus Say	
Scolia nobilitata Fabricius	
2 morphospecies of *Timulla* spp. Ashmead	
Vespula flavopilosa (Jakobson)	
V. maculifons (Buysson)	
V. squamosa (Dury)	

Table E.2: Common forest substrates whose reflectance was measured for the avian visual perception trait categorization.

Forest	Region
Acer saccharum Marsh.	leaves, bark, lichen and moss on bark
Cichorium intybus L.	flowers, sepals, and leaves
Fraxinus americana L.	leaves
Gleditsia triacanthos L.	lichen on bark
Helianthus spp. L.	flowers, sepals, and leaves
Liriodendron tulipifera L.	leaves
Lonicera spp. L.	leaves
Platanus occidentalis L.	leaves
Quercus velutina Lam.	leaves
Sassafras albidum (Nutt.)	leaves
Smilax spp. L.	leaves
Ulmus rubra Muhl.	leaves
Verbesina alternifolia (L.)	flowers and leaves

Appendix F: Colorimetric variables for use in the avian visual perception functional trait categorization

Table F.1: Colorimetric variables (23 total) calculated for beetles with R package "pavo" for use in the avian visual perception functional trait categorization. Abbreviations for each colorimetric variable are also given.

Colorimetric variables
Total brightnesss, B1
Mean brightness, B2
Intensity, B3
Chroma in UV range (lambda min – 400 nm), S1.UV
Chroma in violet range (lambda min – 415 nm), S1.violet
Chroma, in blue range (400 nm – 510 nm), S1.blue
Chroma in green range (510 nm – 605 nm), S1.green
Chroma in yellow range (550 nm – 625 nm), S1.yellow
Chroma in red range (605 nm – lambda max.), S1.red
Spectral saturation (Rmax/Rmin), S2
Chroma, S3
Spectral purity, S4
Chroma, S5
Contrast, S6
Spectral saturation, S7
Chroma, S8
Carotenoid chroma, S9
Peaky chroma, S10*
Peak wavelength, hue, H1
Hue, H2*
Hue, H3
Hue, H4
Hue, H5

*Not used in analysis because calculations could not be made for all beetle species

More details on colorimetric variable description are given in the pavo package description (Maia et al. 2013) and Montgomerie (2006).

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Appendix G: Standardized coefficients from multiple regression of functional redundancy (FR) and response diversity (RD) of each functional group (FG) with fragmentation.

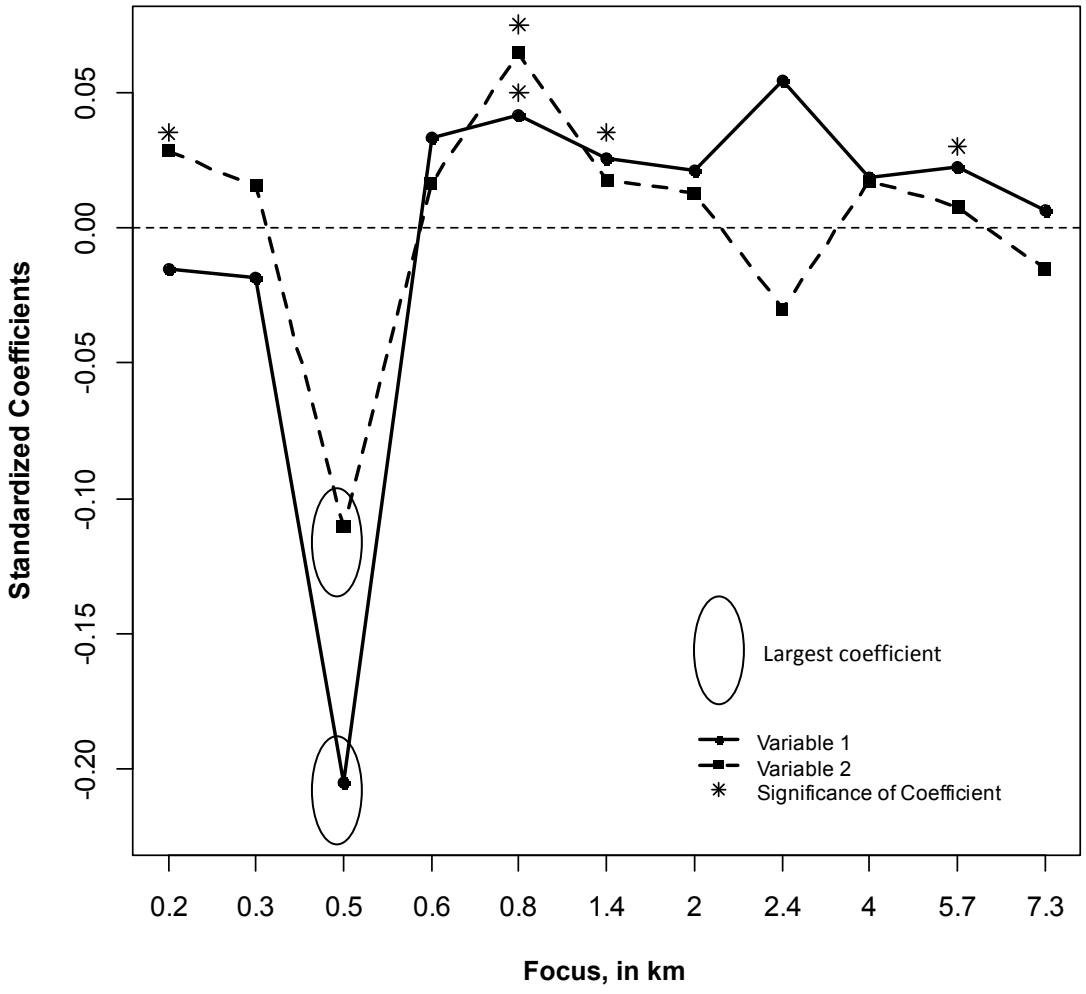

Figure G.1: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG1 functional redundancy. Variable 1: aggregation index, mean patch area, proportion landscape, or total area; Variable 2: edge density, landscape division index, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index.

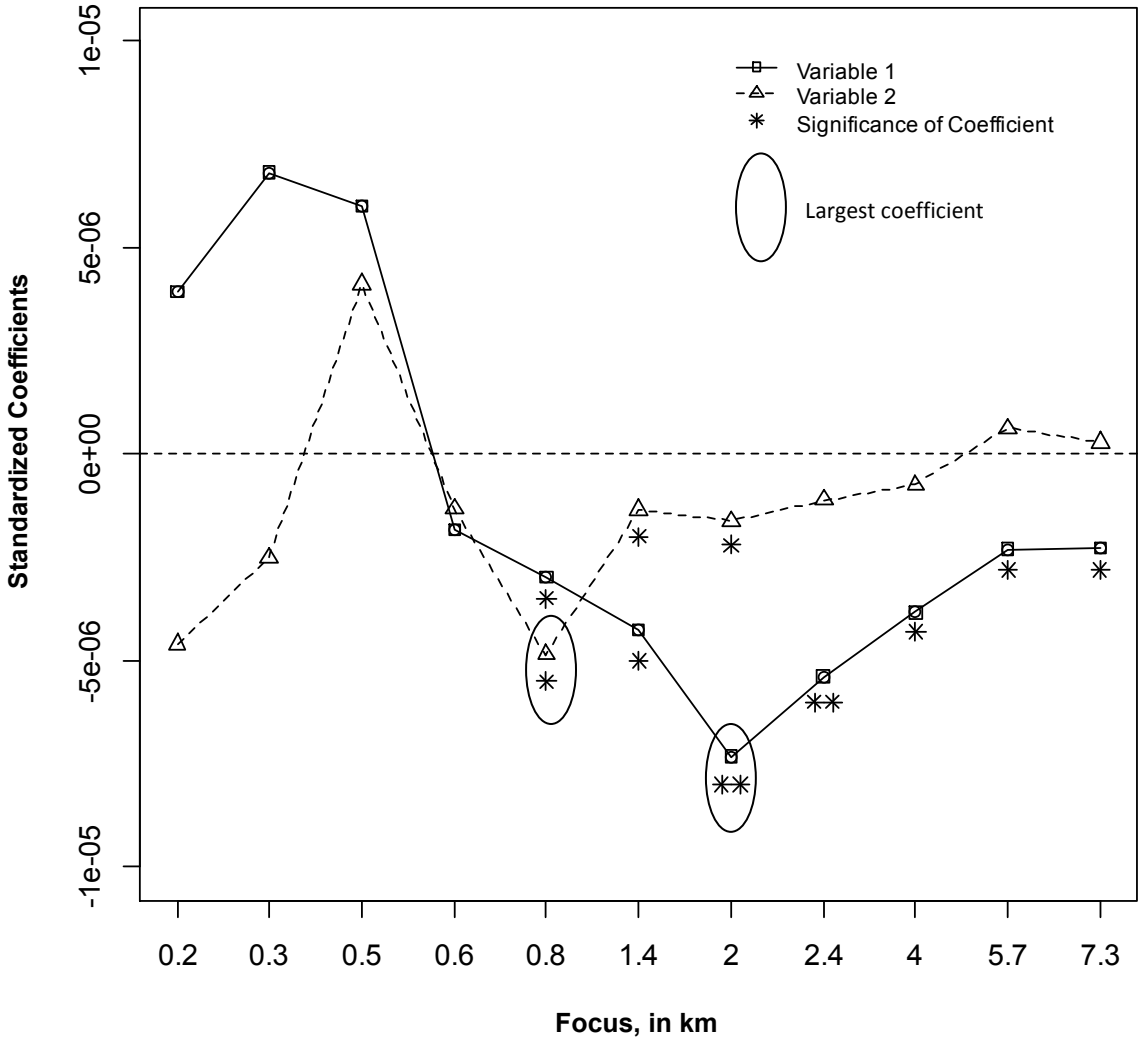

Figure G.2: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG1 response diversity. Variable 1: aggregation index or total area; Variable 2: edge density, landscape division index, landscape shape index, mean fractal dimension index, mean shape index.

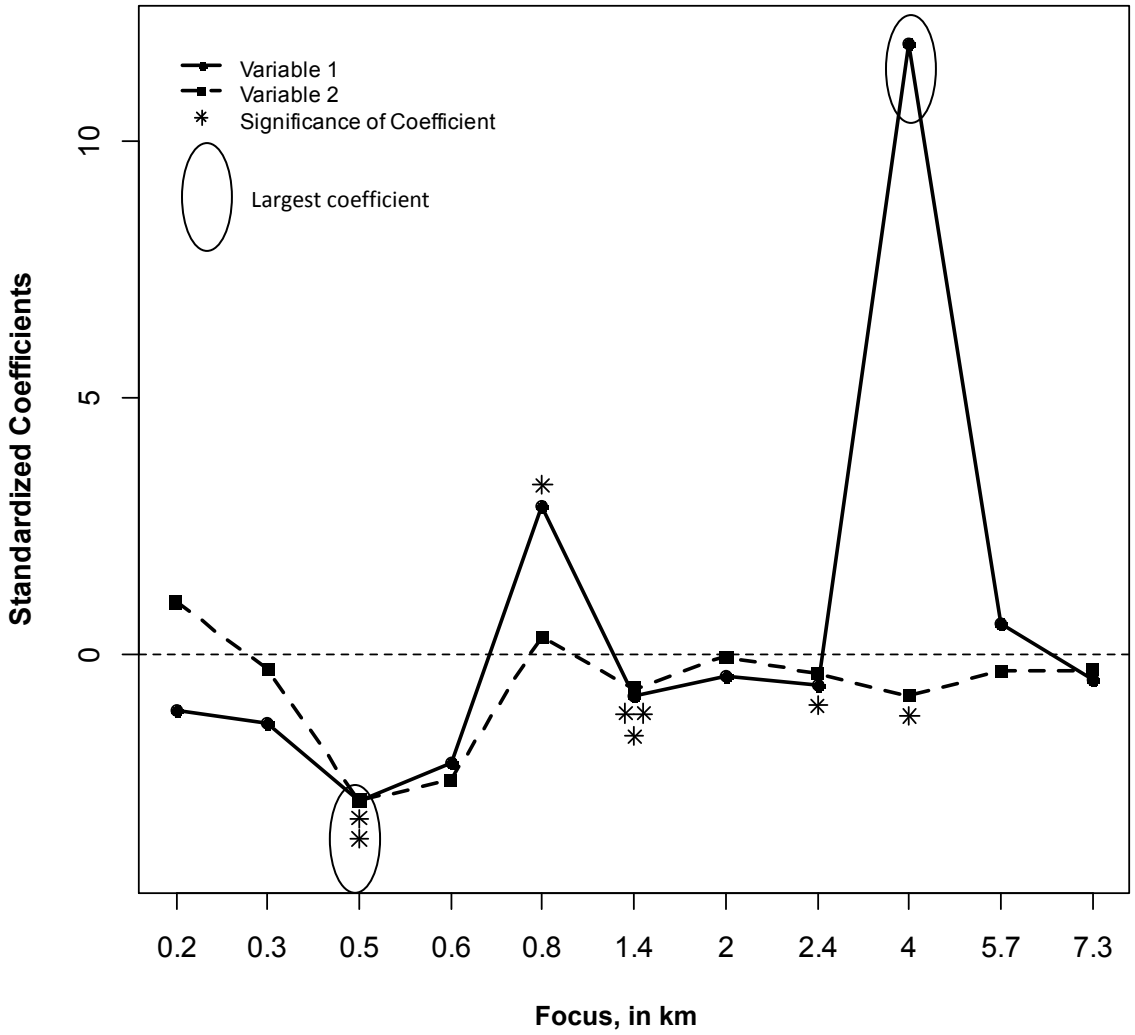

Figure G.3: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG2 functional redundancy. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, or mean shape index.

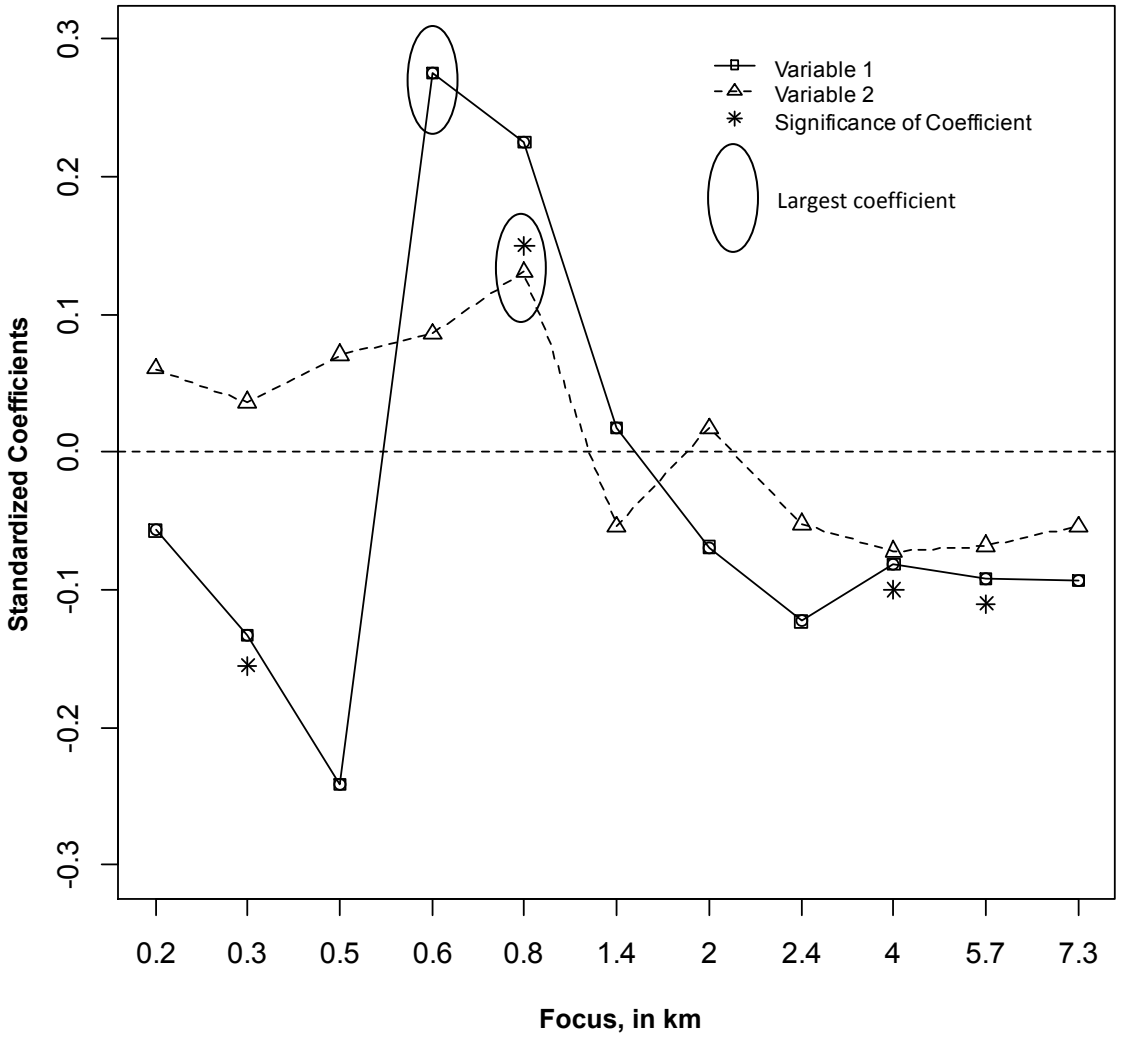

Figure G.4: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG2 response diversity. Variable 1: aggregation index, mean patch area, proportion landscape, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean shape index.

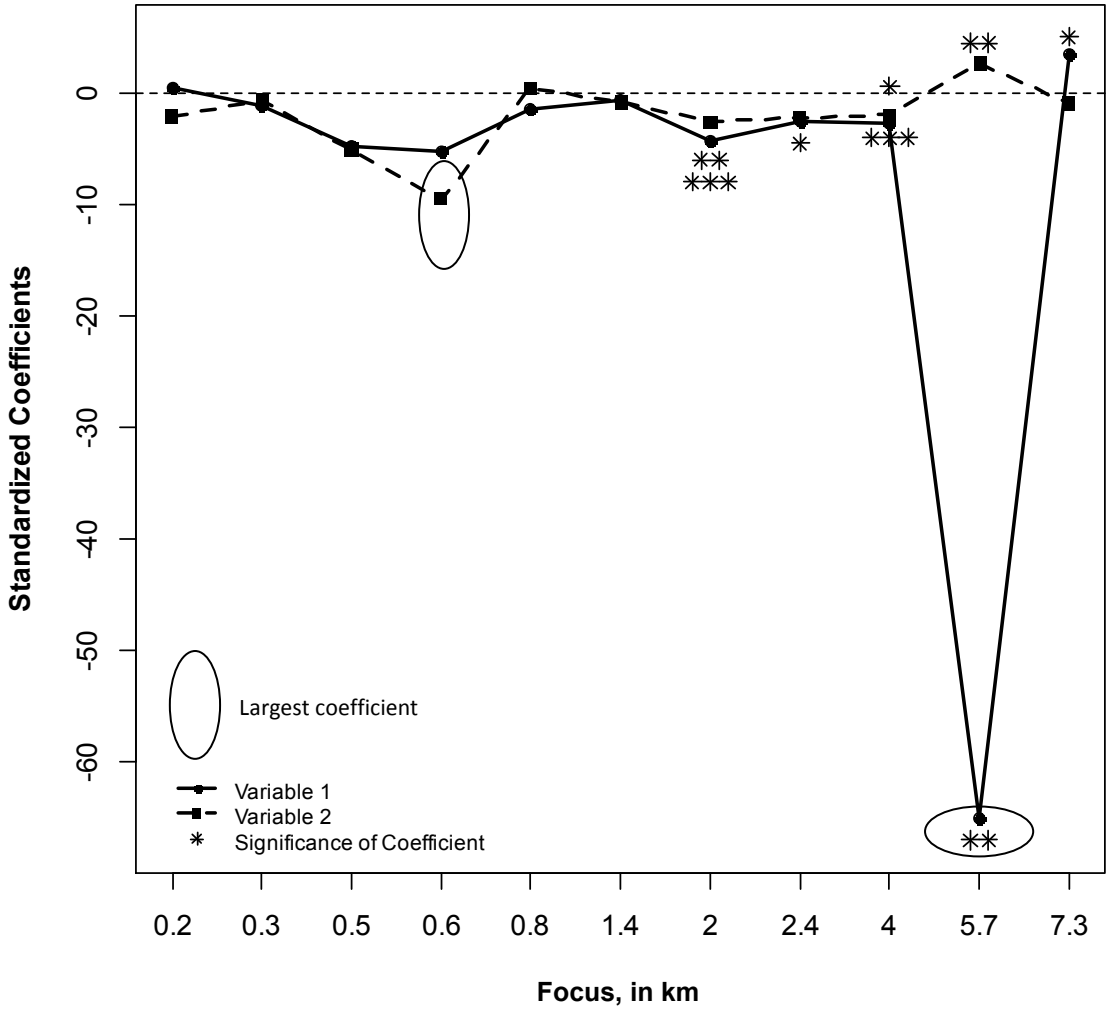

Figure G.5: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG3 functional redundancy. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index.

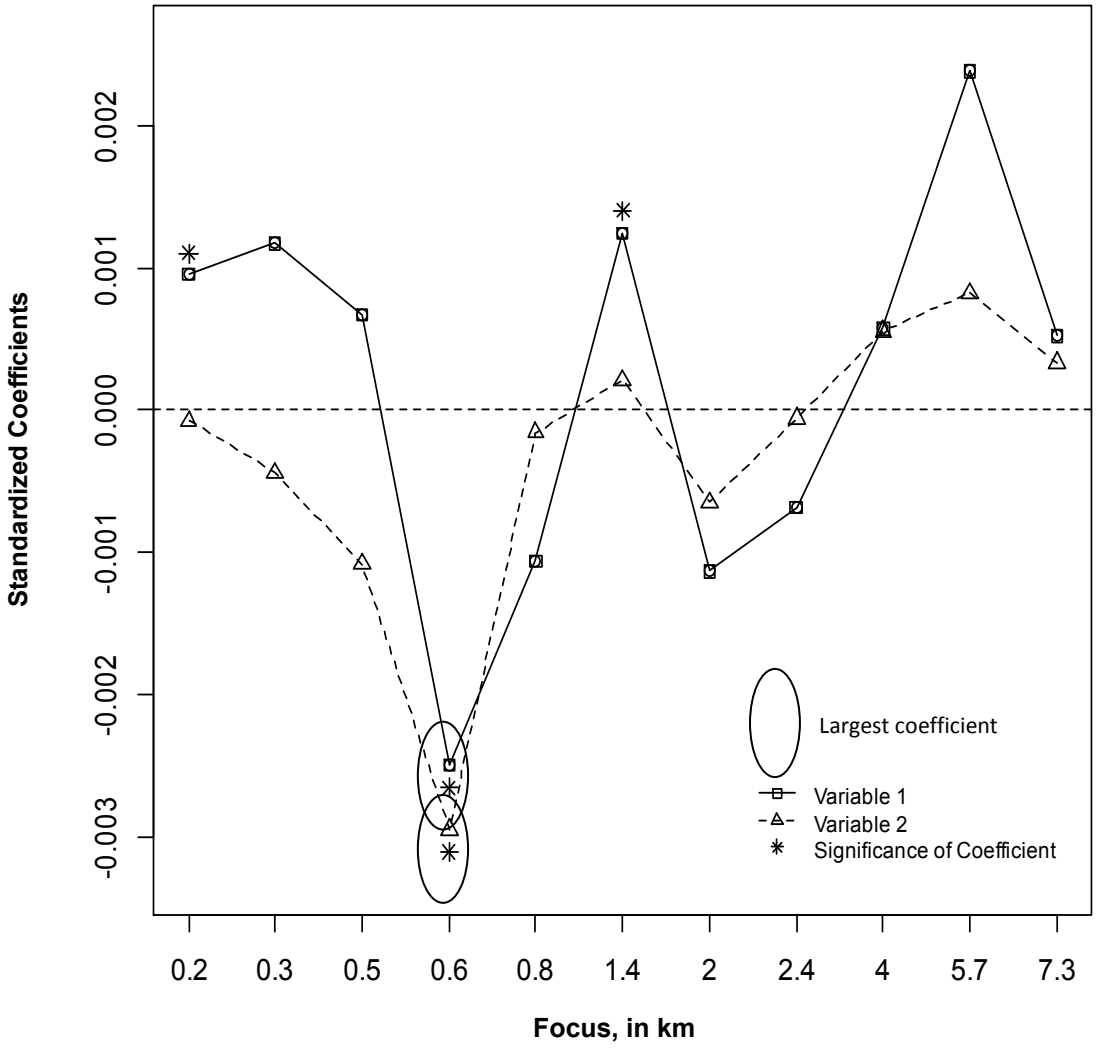

Figure G.6: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of wood-boring beetle FG3 response diversity. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index.

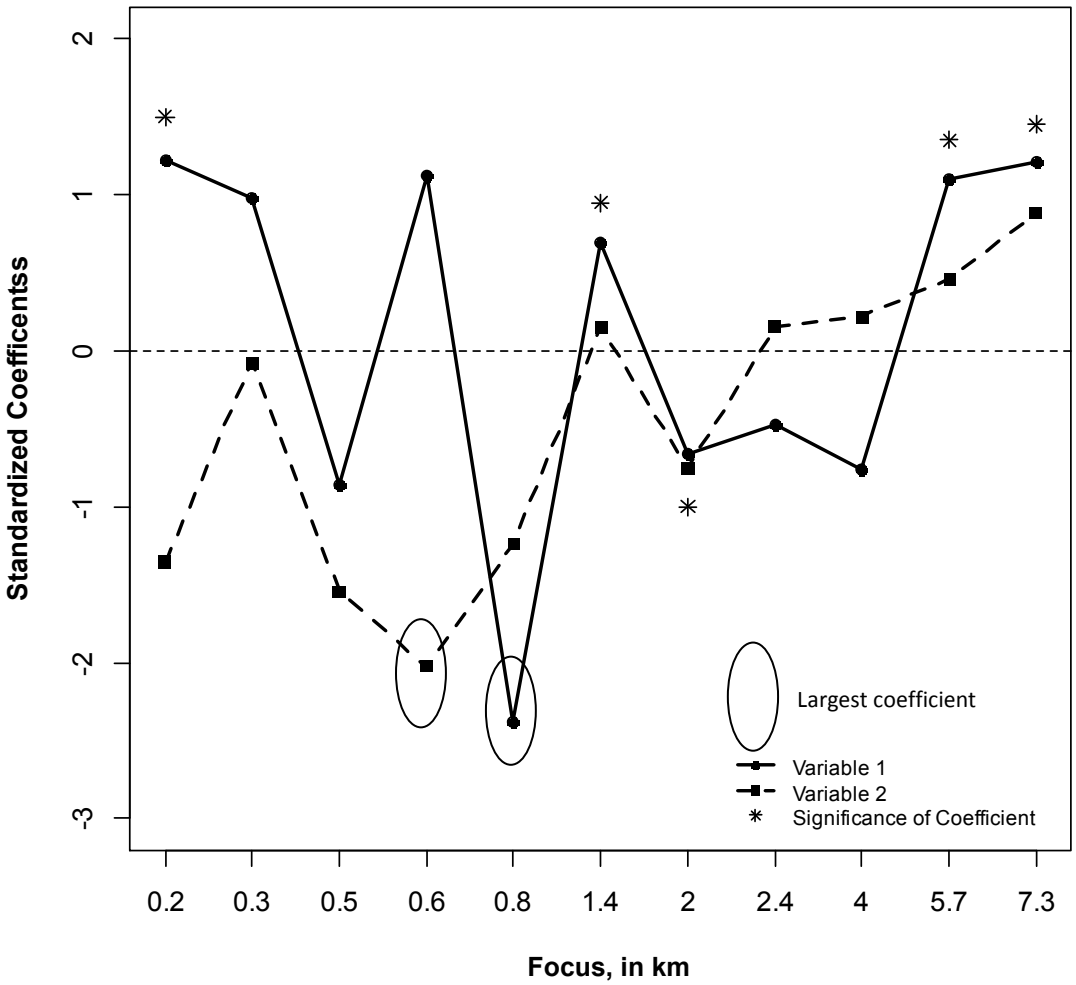

Figure G.7: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGA functional redundancy. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, mean fractal dimension index, mean perimeter area ratio, mean shape index.

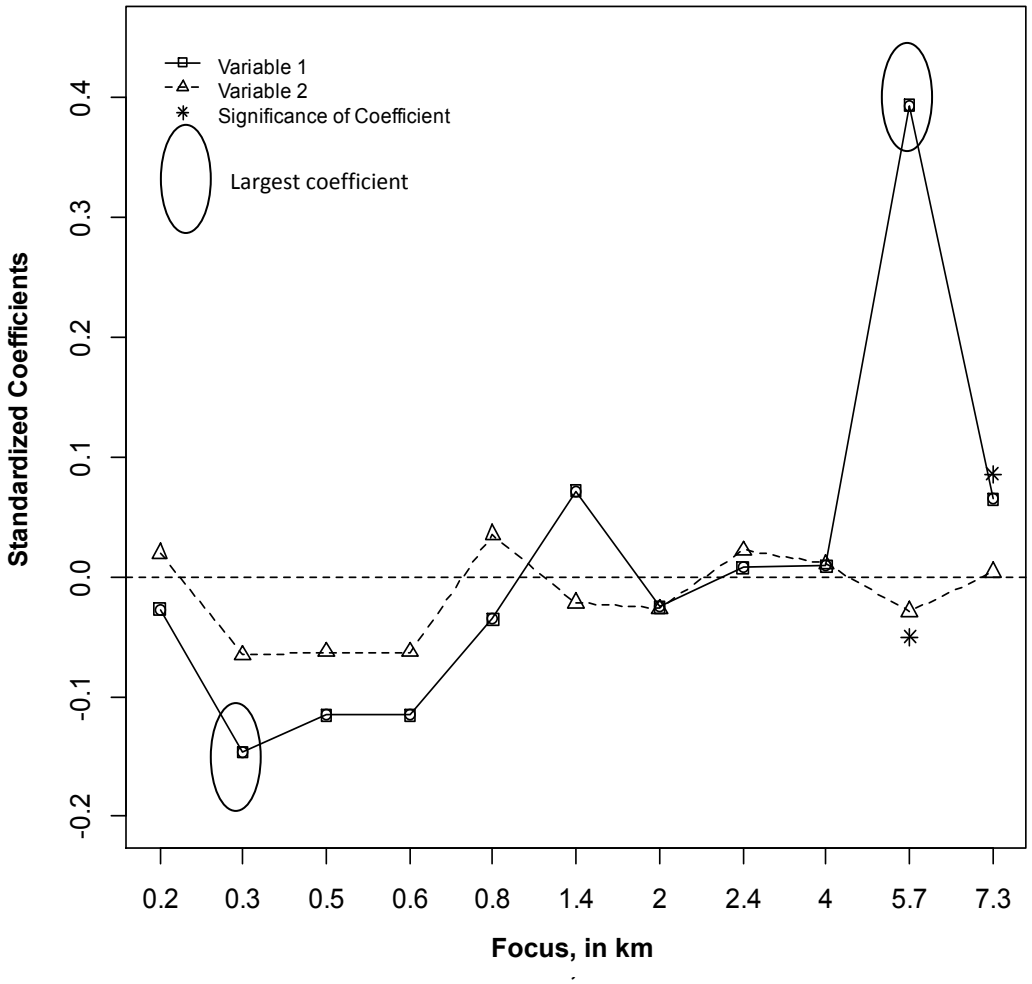

Figure G.8: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGA response diversity. Variable 1: aggregation index, mean patch area, proportion landscape, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, or mean shape index.

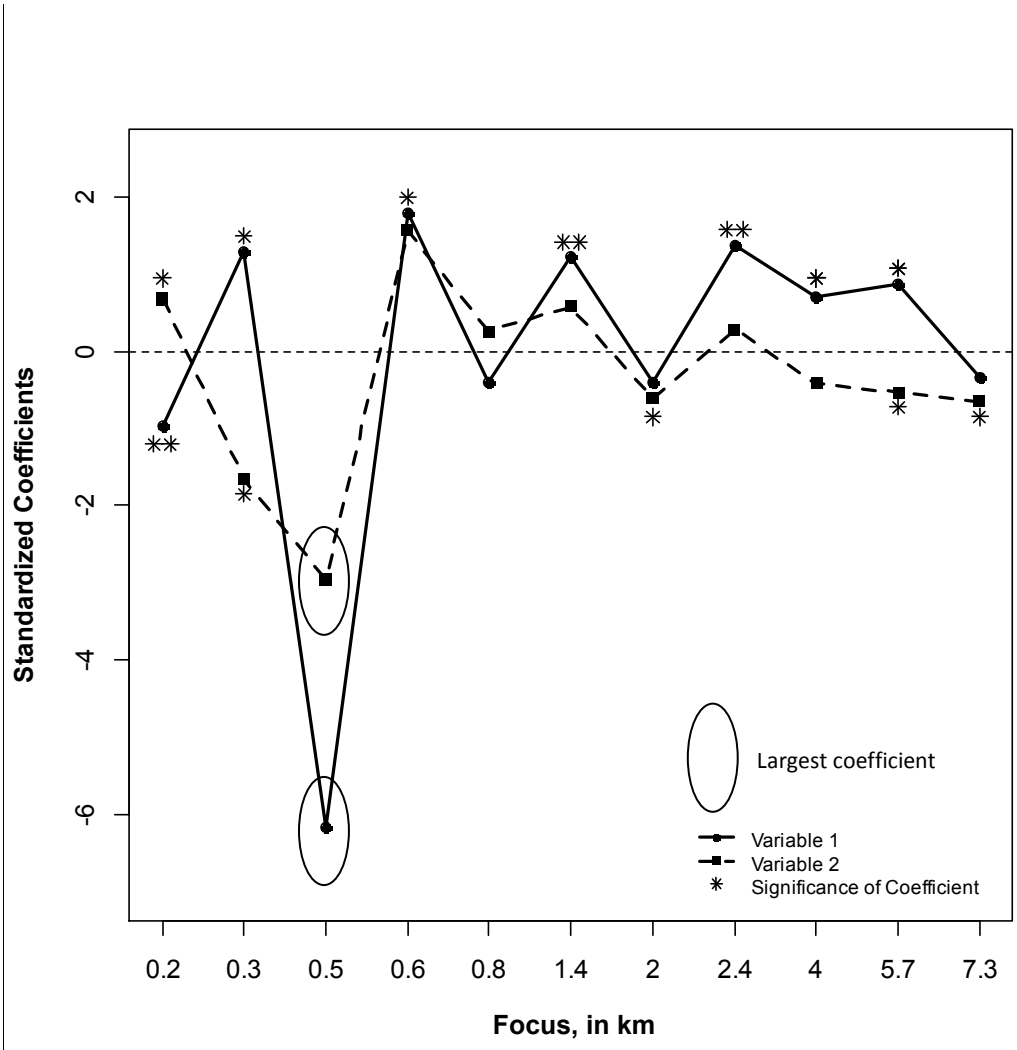

Figure G.9: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGB functional redundancy. Variable 1: aggregation index, proportion landscape, or total area; Variable 2: edge density, landscape division index, mean fractal dimension index, mean shape index, or total edge.

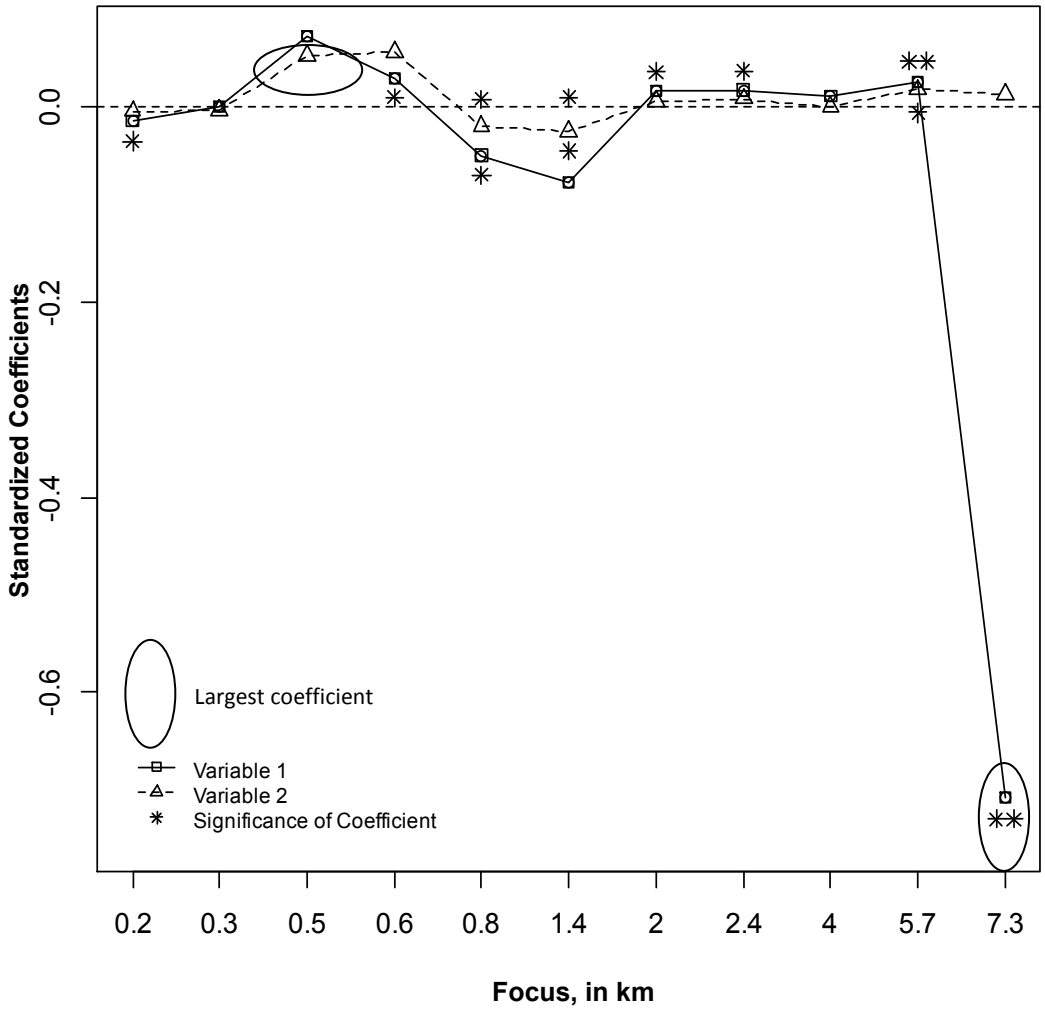

Figure G.10: Standardized coefficients of Variable 1 and Variable 2 in multiple regressions of predator FGB response diversity. Variable 1: aggregation index, mean patch area, or total area; Variable 2: edge density, landscape shape index, mean fractal dimension index, mean perimeter area ratio, or mean shape index.

Appendix H: Proportion of variance explained by models (redundancy analysis (RDA) and multiple regression.

Table H.1: Proportion of variance explained by model (proportion explained by constrained axes (RDA) or R-squared value (multiple regression). Selected spatial foci are highlighted in gray.

Analytical focus	2	3	4	5	6	7	8	9	10	11	12
Cerambycid community (RDA)	0.07036	0.07645	0.2691	0.2628	0.381	0.306	0.3132	0.3085	0.4128	0.2854	0.3297
Predator community (RDA)	0.1417	0.165	0.2948	0.2165	0.3136	0.2044	0.2276	0.2225	0.1812	0.264	0.2833
FG1 RD (multiple regression)	0.1058	0.1684	0.4154	0.2484	0.369	0.2912	0.3455	0.3588	0.2932	0.2581	0.2616
FG2 RD (multiple regression)	0.09851	0.2183	0.315	0.2741	0.4184	0.3767	0.3065	0.2486	0.2992	0.3225	0.3191
FG3 RD (multiple regression)	0.2151	0.221	0.4578	0.3788	0.3442	0.3109	0.2237	0.1907	0.141	0.0869	0.0523
FG1 FR (multiple regression)	0.2107	0.1461	0.3819	0.2997	0.511	0.3555	0.3434	0.3604	0.2966	0.3028	0.3615
FG2 FR (multiple regression)	0.08216	0.144	0.3375	0.2434	0.5077	0.4175	0.255	0.3321	0.3777	0.3586	0.3315
FG3 FR (multiple regression)	0.1988	0.1753	0.2777	0.3321	0.4803	0.4082	0.5437	0.4838	0.533	0.5717	0.492
FGA RD (multiple regression)	0.1008	0.05245	0.1357	0.0894	0.09991	0.1253	0.1911	0.07811	0.0832	0.2508	0.3855
FGB RD (multiple regression)	0.2204	0.3409	0.4028	0.4247	0.4444	0.2601	0.2729	0.3757	0.2304	0.473	0.395
FGA FR (multiple regression)	0.2298	0.1635	0.36	0.2771	0.4527	0.2858	0.4423	0.2715	0.2863	0.4131	0.327
FGB FR (multiple regression)	0.2785	0.2656	0.3798	0.2869	0.4164	0.4241	0.4457	0.3587	0.4474	0.4633	0.4776

Table H.2: Landscape focus and landscape metrics selected for threshold analyses at the community and functional group levels.

	Focus: landscape metrics selected
Cerambycid community (RDA)	Focus 10: aggregation index, mean frac dim index
Predator community (RDA)	Focus 6: total area, edge density
FG1 RD (multiple regression)	Focus 4: aggregation index, edge density
FG2 RD (multiple regression)	Focus 6: proportion landscape, edge density
FG3 RD (multiple regression)	Focus 4: aggregation index, edge density
FG1 FR (multiple regression)	Focus 6: aggregation index and edge density
FG2 FR (multiple regression)	Focus 6: mean patch area, landscape shape index
FG3 FR (multiple regression)	Focus 11: aggregation index, mean perim area ratio
FGA RD (multiple regression)	Focus 12: mean patch area, edge density
FGB RD (multiple regression)	Focus 11: total area, mean shape index
FGA FR (multiple regression)	Focus 6: total area, edge density
FGB FR (multiple regression)	Focus 12: total area, mean shape index

Appendix I: Dendrograms of wood-boring beetle (Coleoptera: Cerambycidae) and predator beetle functional groupings.

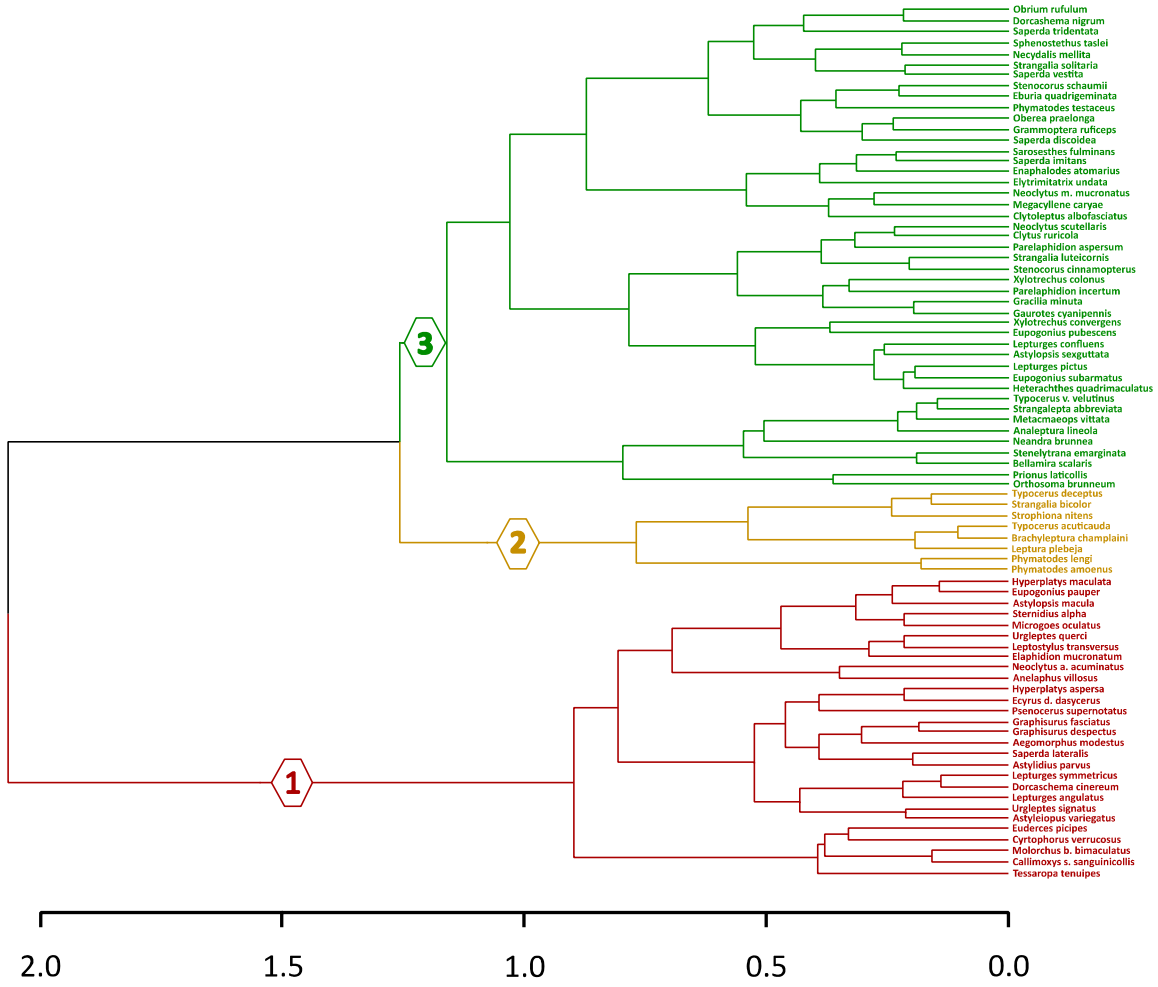

Figure I.1. Dendrogram of wood-boring beetle functional groups.

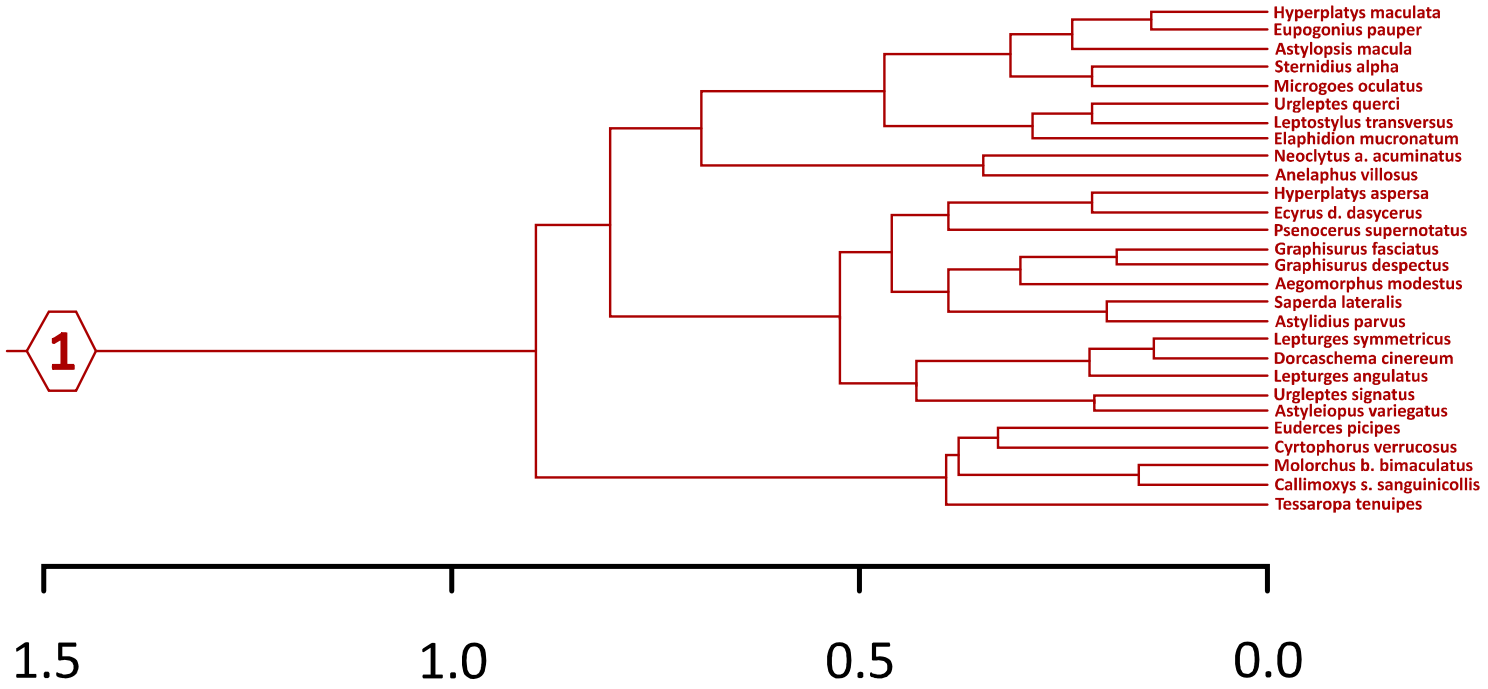

Figure I.2: Branch of wood-boring beetle functional group 1 (FG1).

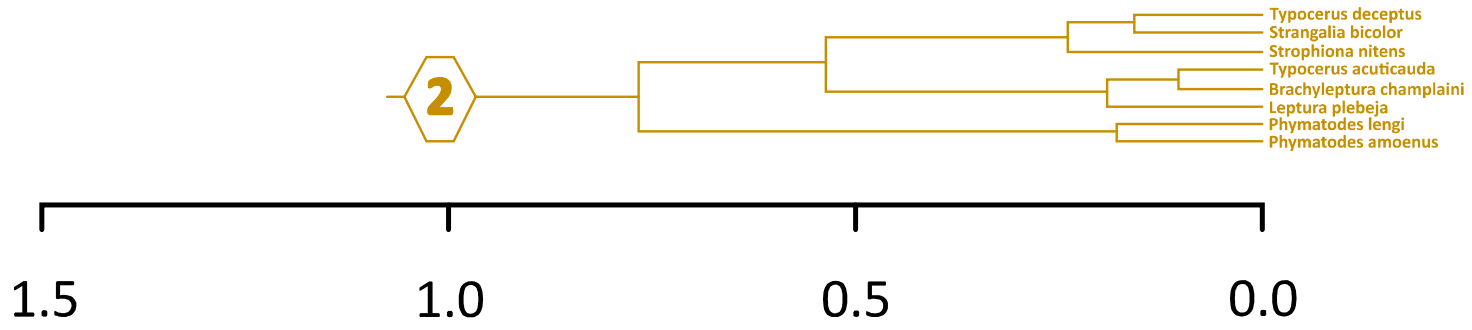

Figure I.3: Branch of wood-boring beetle functional group 2 (FG2).

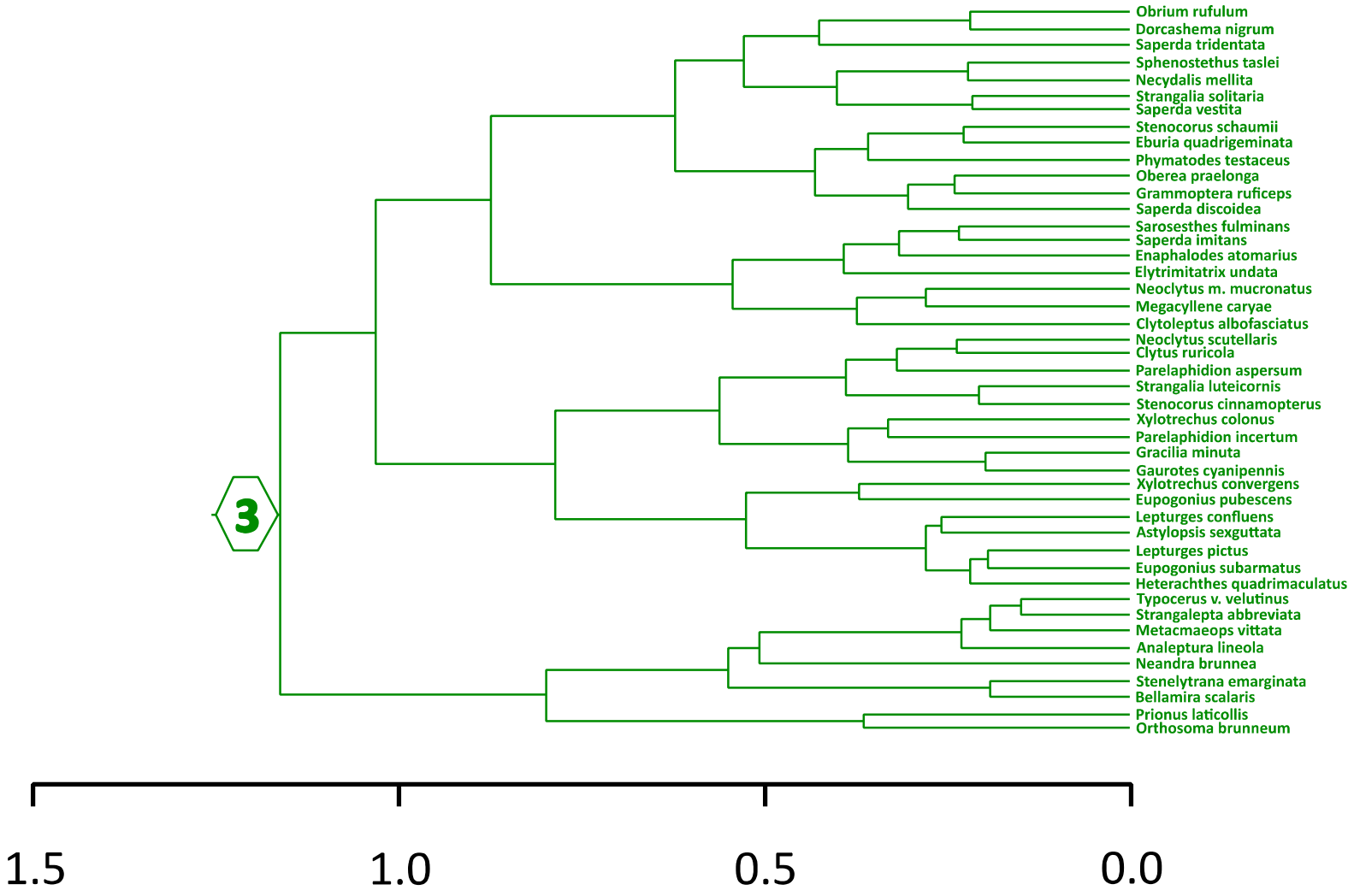

Figure I.4: Branch of wood-boring beetle functional group 3 (FG3).

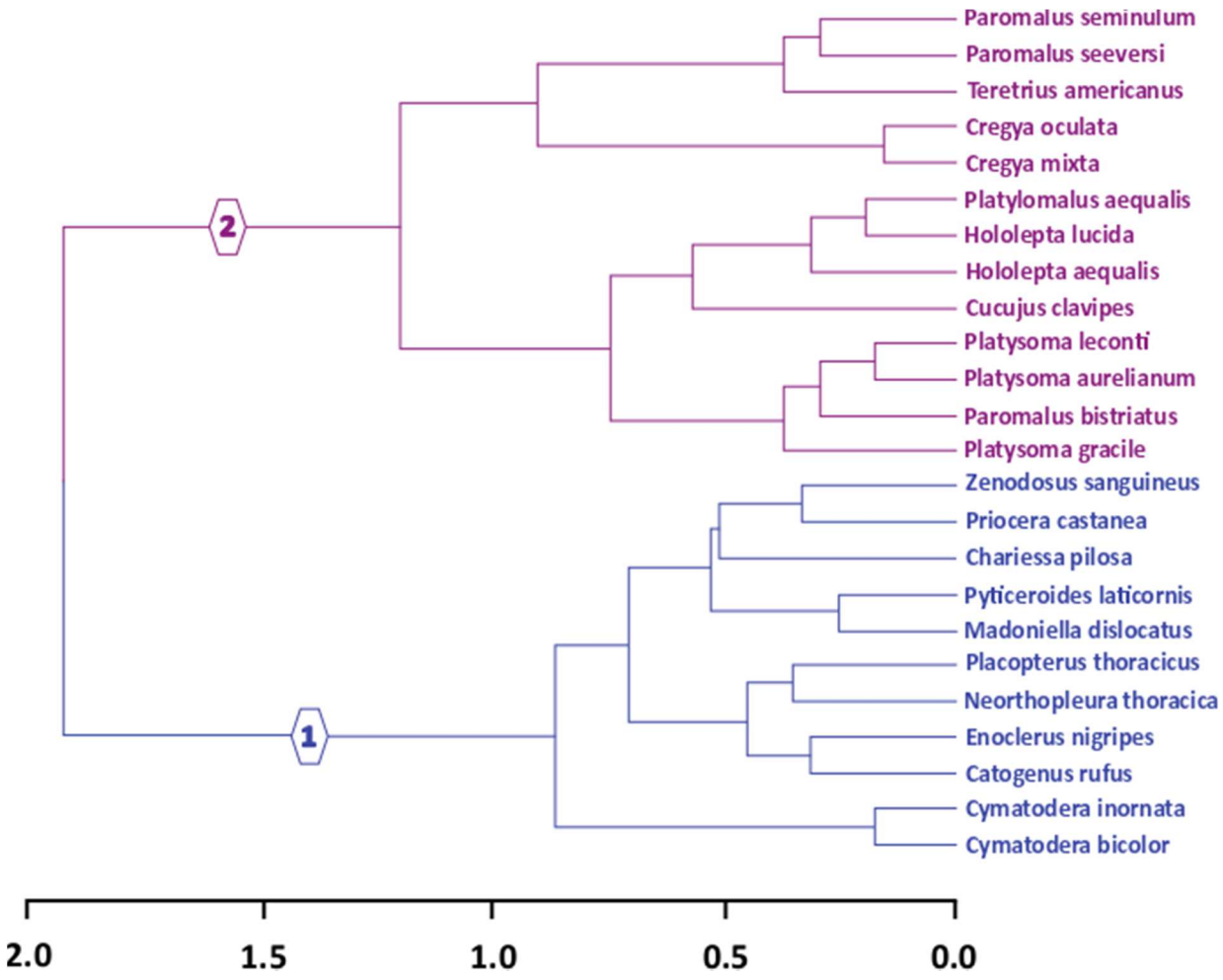

Figure I.5: Dendrogram of predator beetle functional groups.

Appendix J: Redundancy analysis (RDA) triplots of wood-boring beetle functional diversity indices (FDiv, FEve, and FRic) with landscape. Only the significant relationships are given.

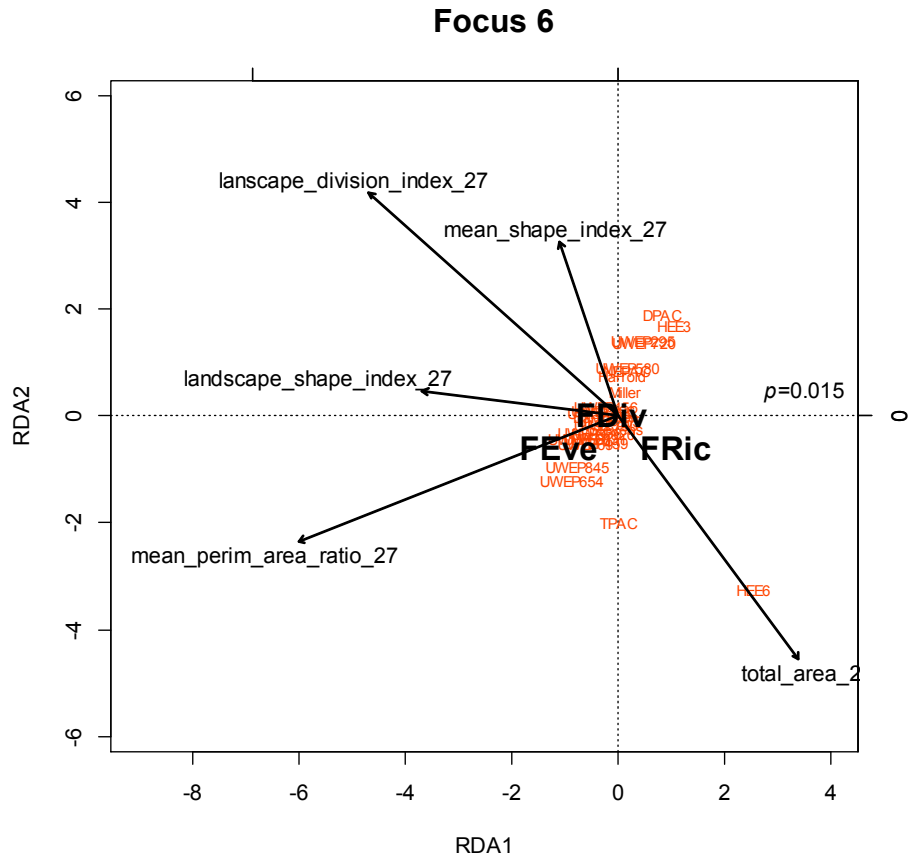

Figure J.1: Redundancy analysis (RDA) triplot at an analytical focus of 0.81 km (Focus 6). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

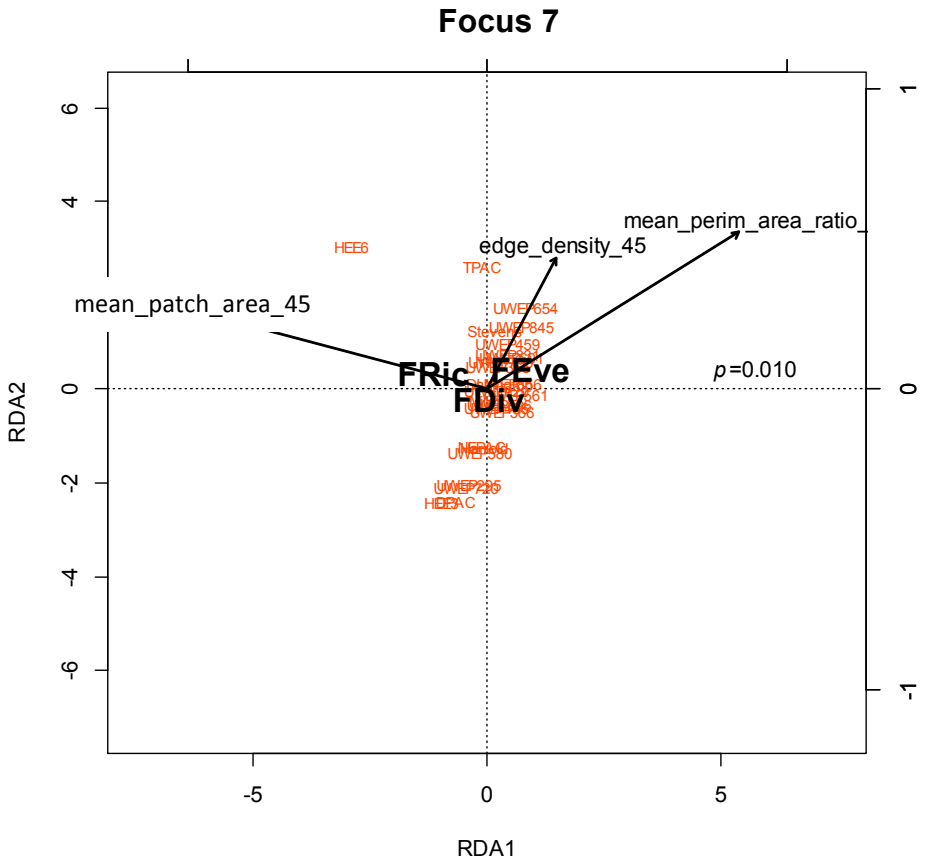

Figure J.2: Redundancy analysis (RDA) triplot at an analytical focus of 1.35 km (Focus 7). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

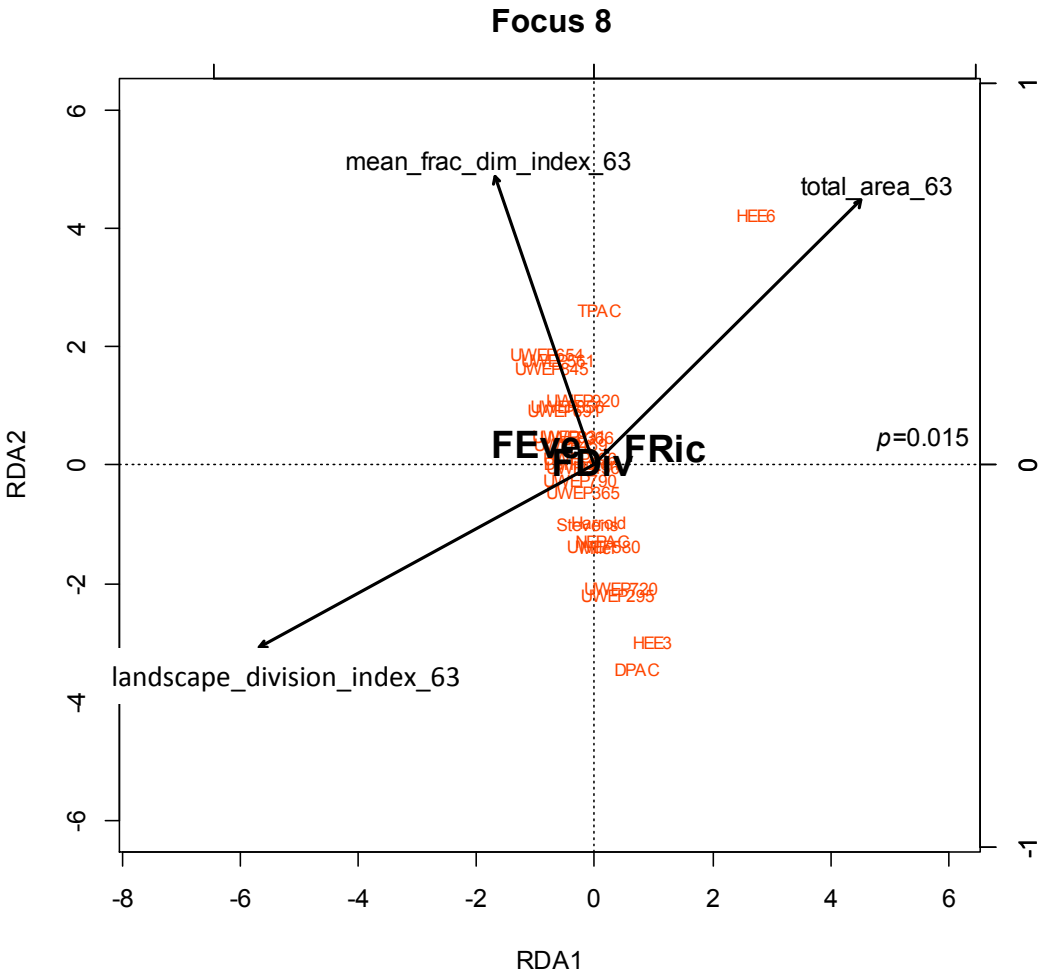

Figure J.3: Redundancy analysis (RDA) triplot at an analytical focus of 1.89 km (Focus 8). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

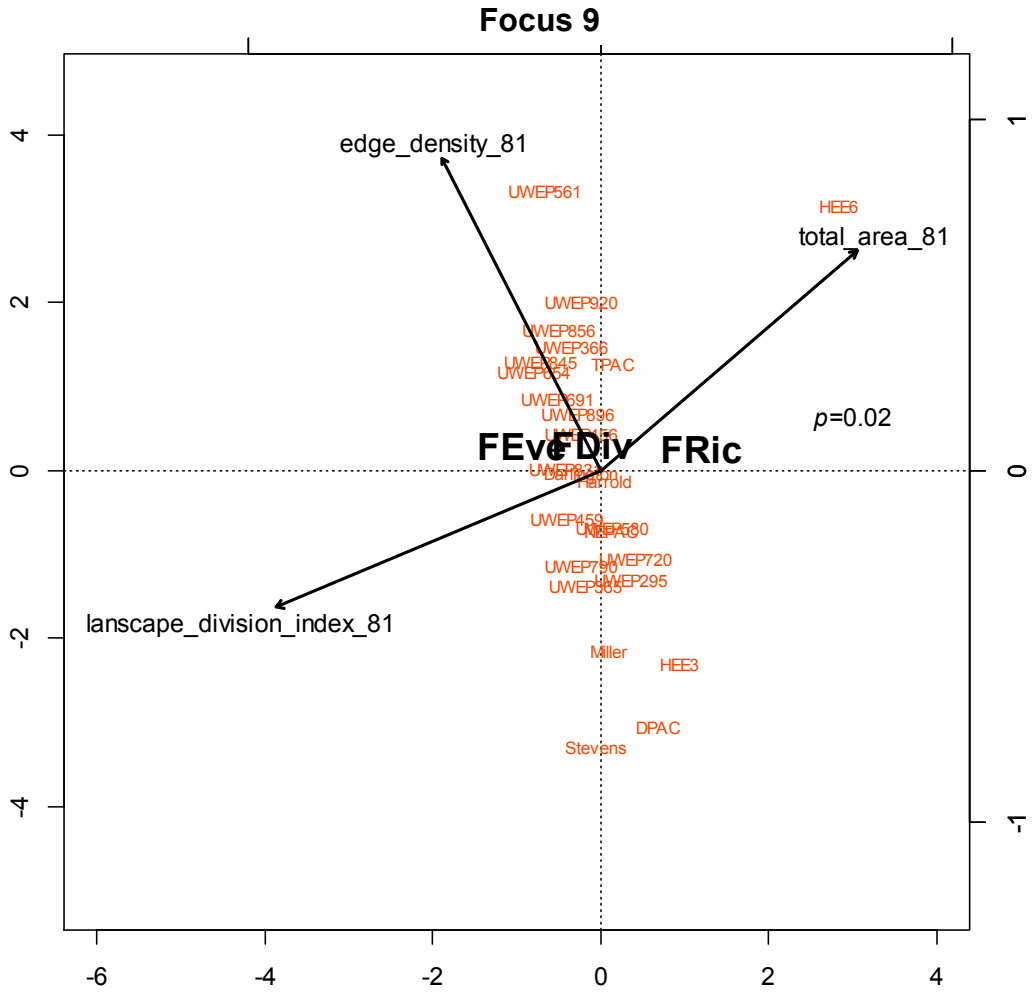

Figure J.4. Redundancy analysis (RDA) triplot at an analytical focus of 2.43 km (Focus 9). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

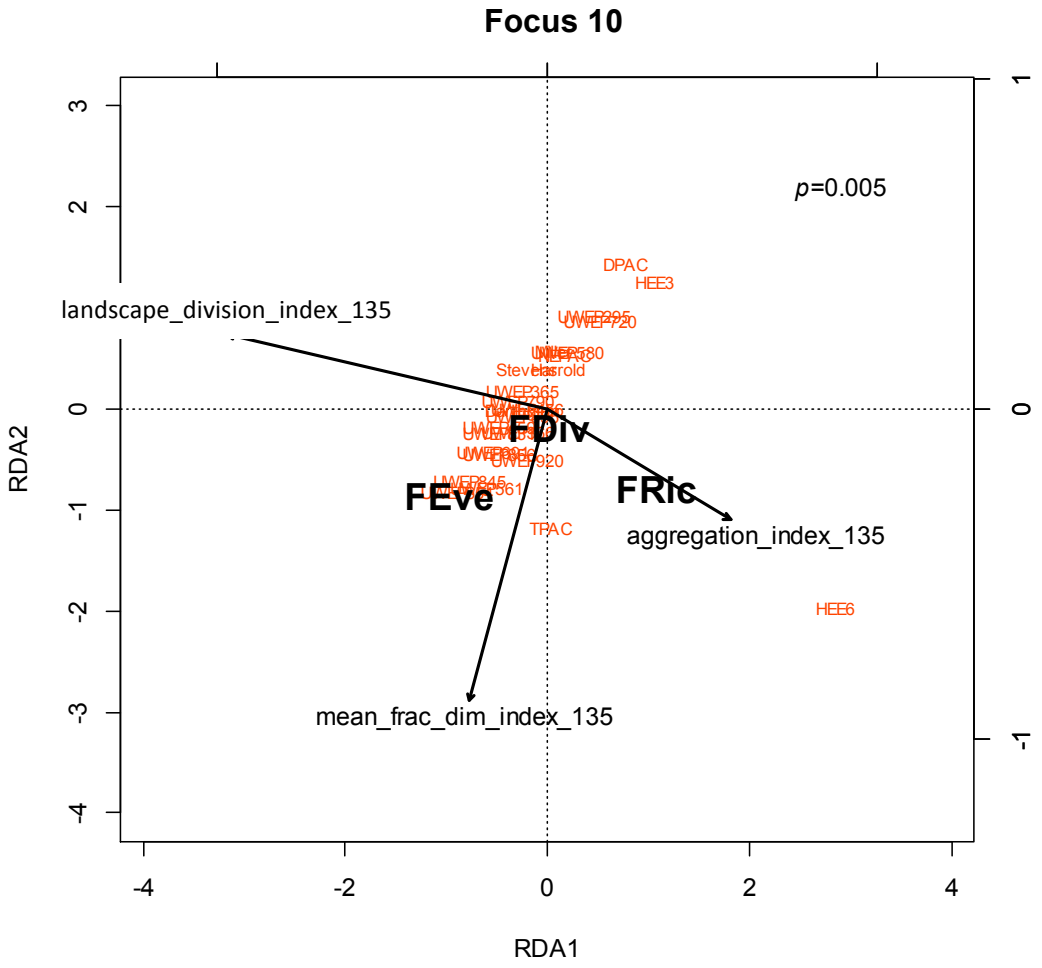

Figure J.5. Redundancy analysis (RDA) triplot at an analytical focus of 4.05 km (Focus 10). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

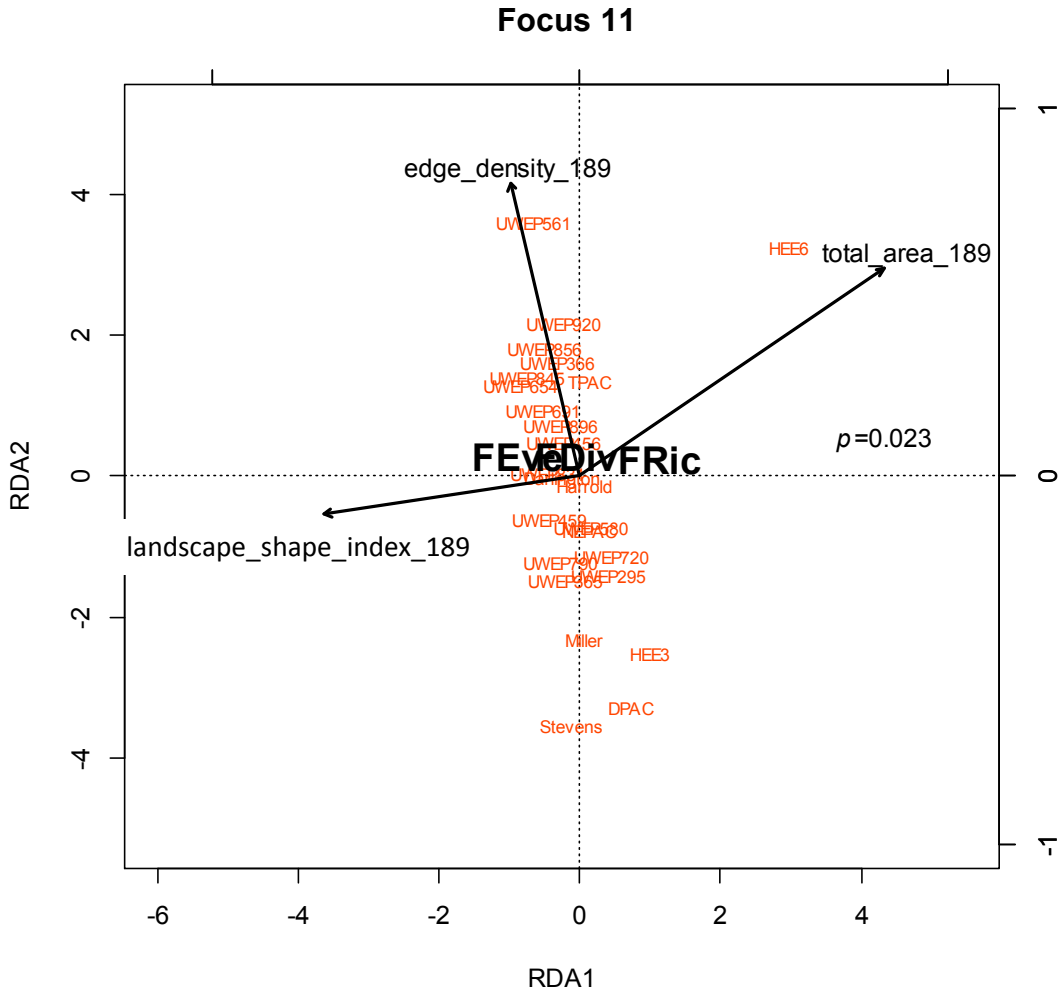

Figure J.6. Redundancy analysis (RDA) triplot at an analytical focus of 5.67 km (Focus 11). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

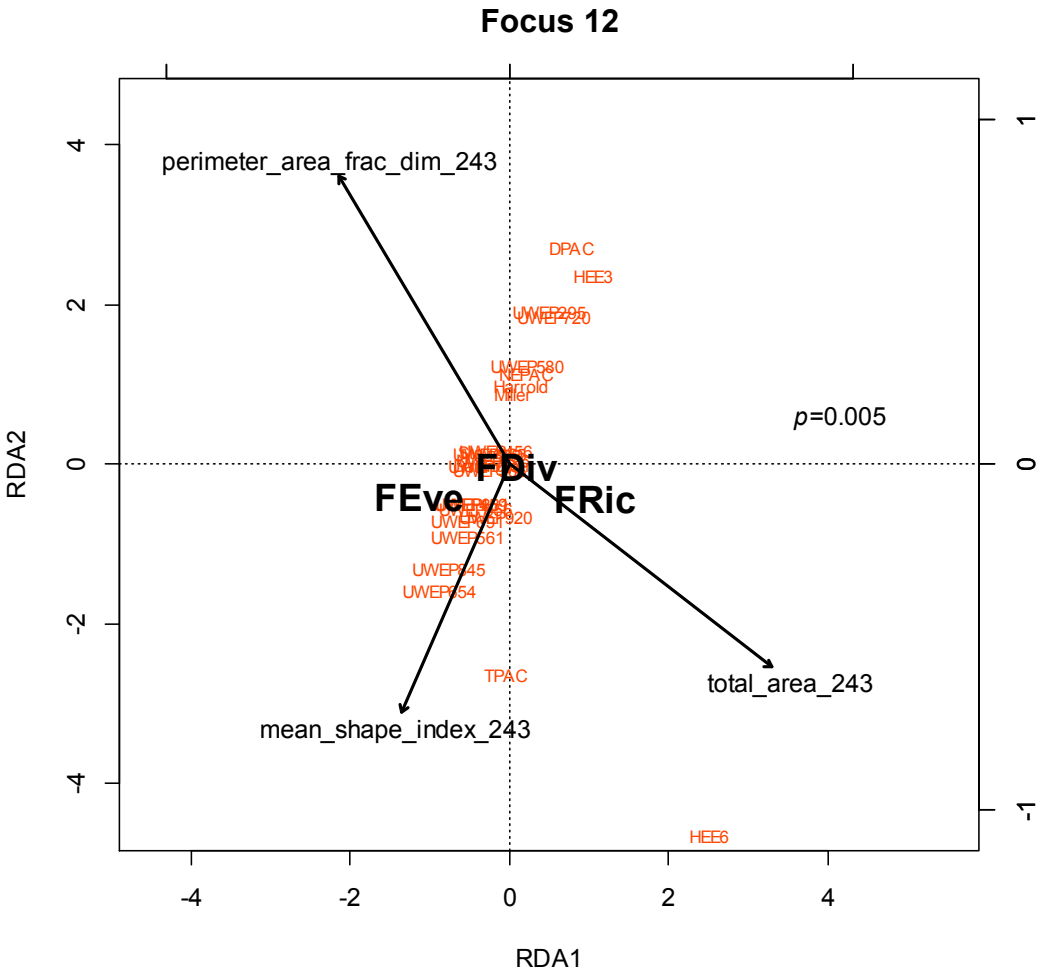

Figure J.7. Redundancy analysis (RDA) triplot at an analytical focus of 7.29 km (Focus 12). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

Appendix K: Redundancy analysis (RDA) triplots of predator beetle functional diversity indices (FDis, FDiv, FEve, and FRic) with landscape. Only the significant relationships are given.

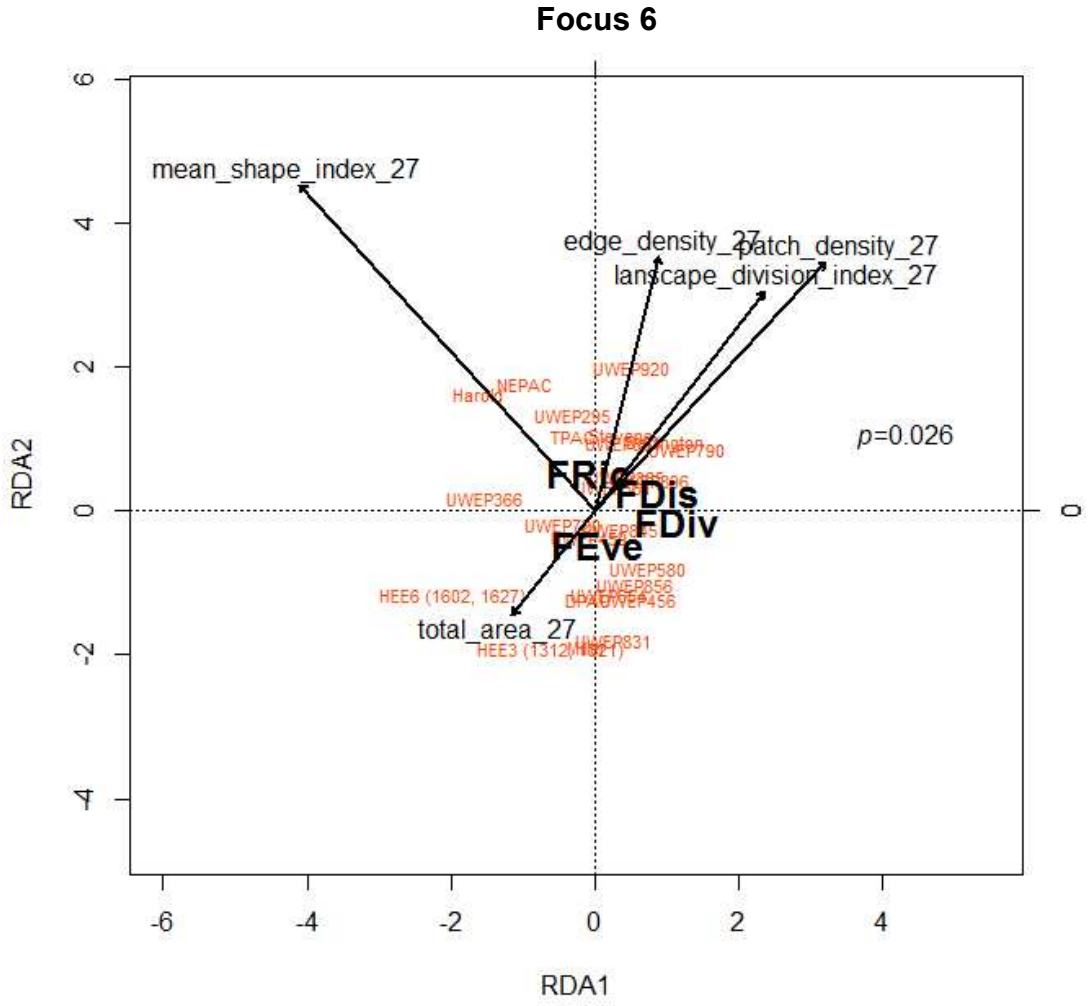

Figure K.1: Redundancy analysis (RDA) triplot at an analytical focus of 0.81 km (Focus 6). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

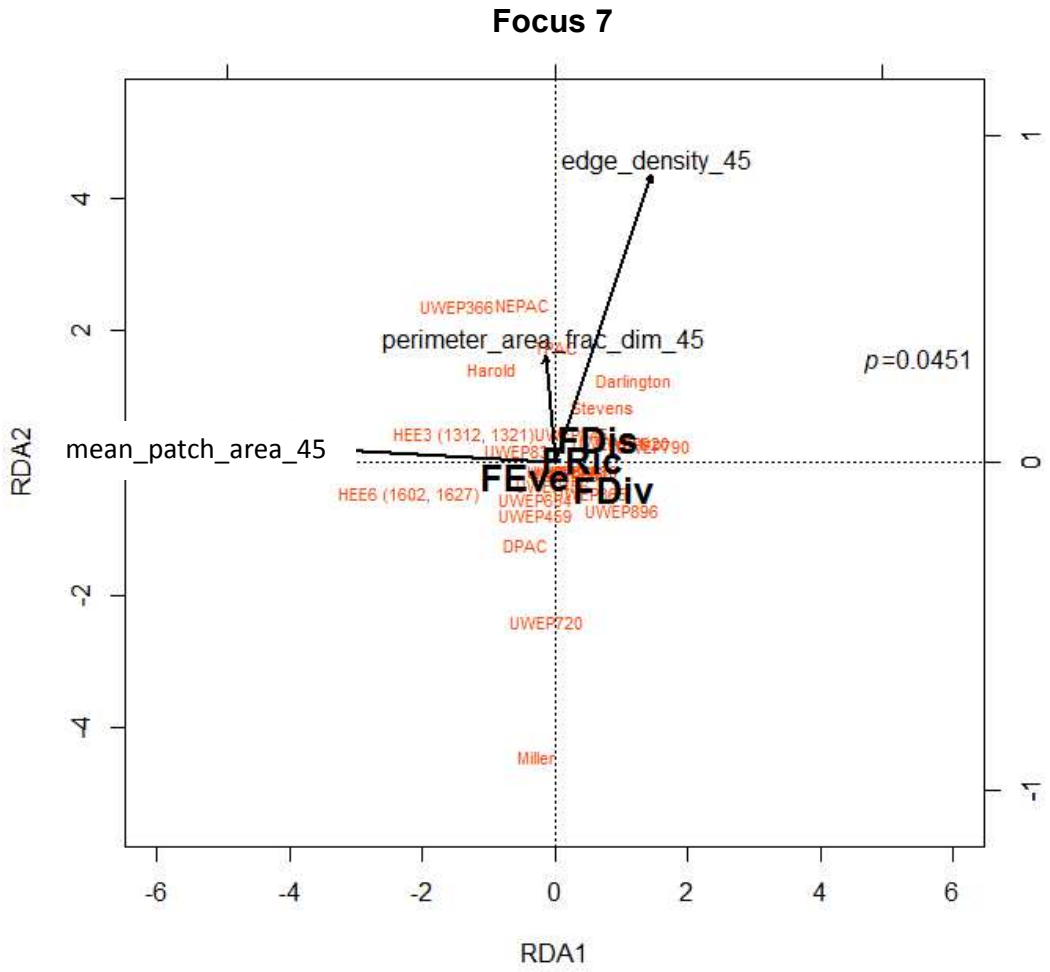

Figure K.2: Redundancy analysis (RDA) triplot at an analytical focus of 1.35 km (Focus 7). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

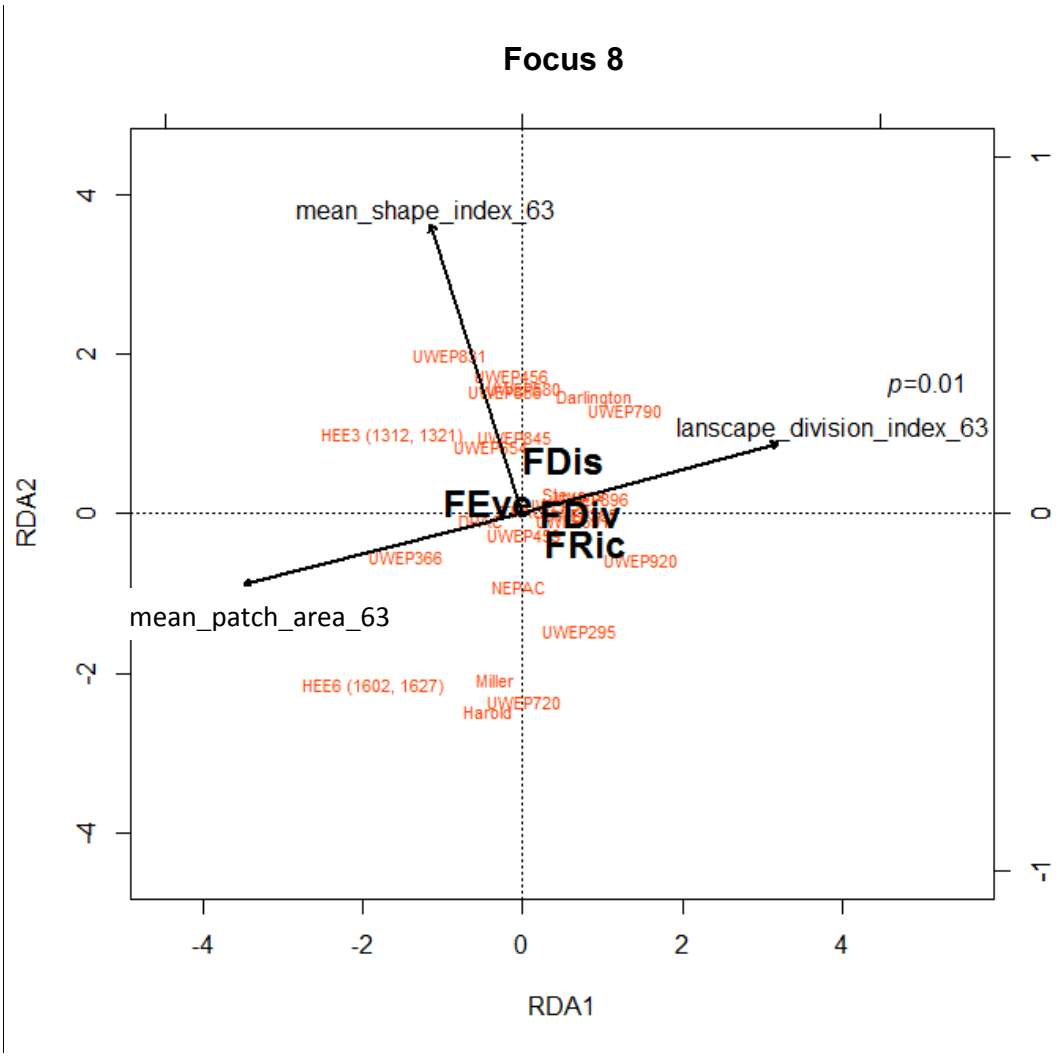

Figure K.3: Redundancy analysis (RDA) triplot at an analytical focus of 1.89 km (Focus 8). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

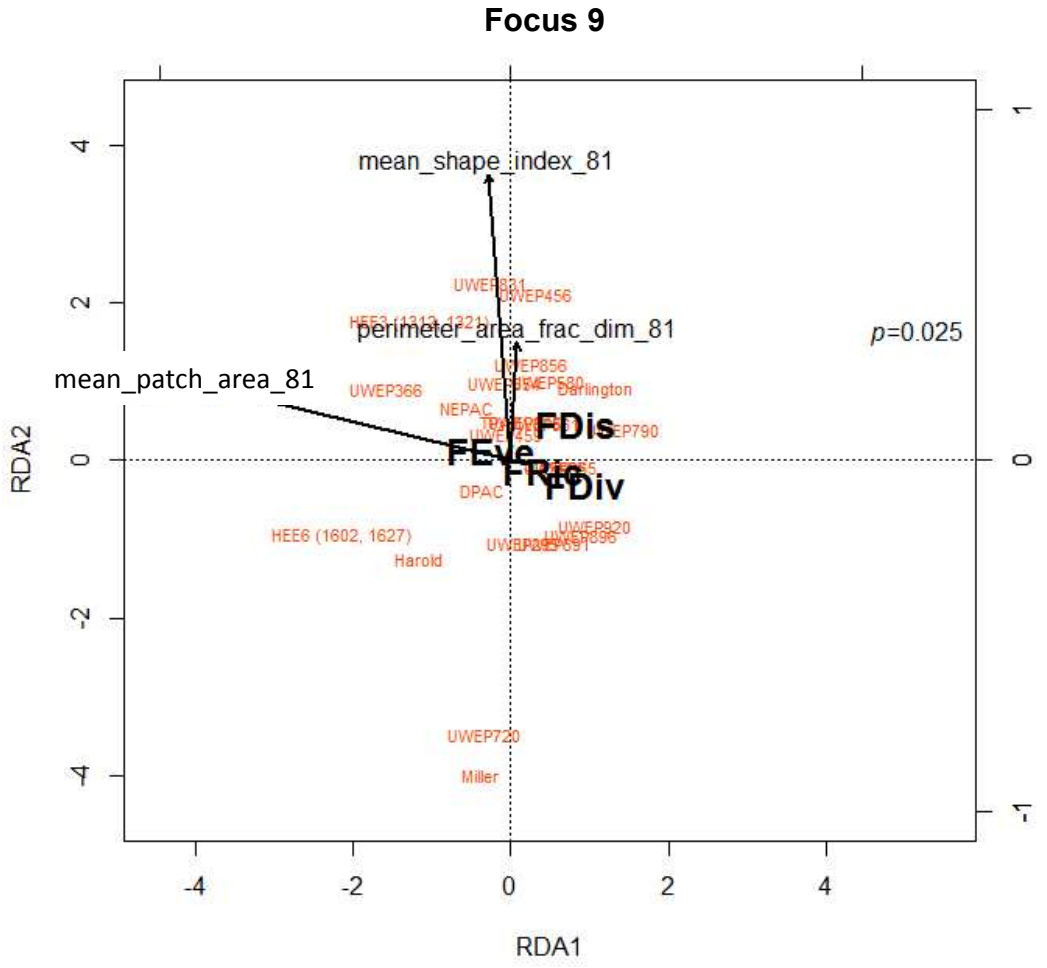

Figure K.4: Redundancy analysis (RDA) triplot at an analytical focus of 2.43 km (Focus 9). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

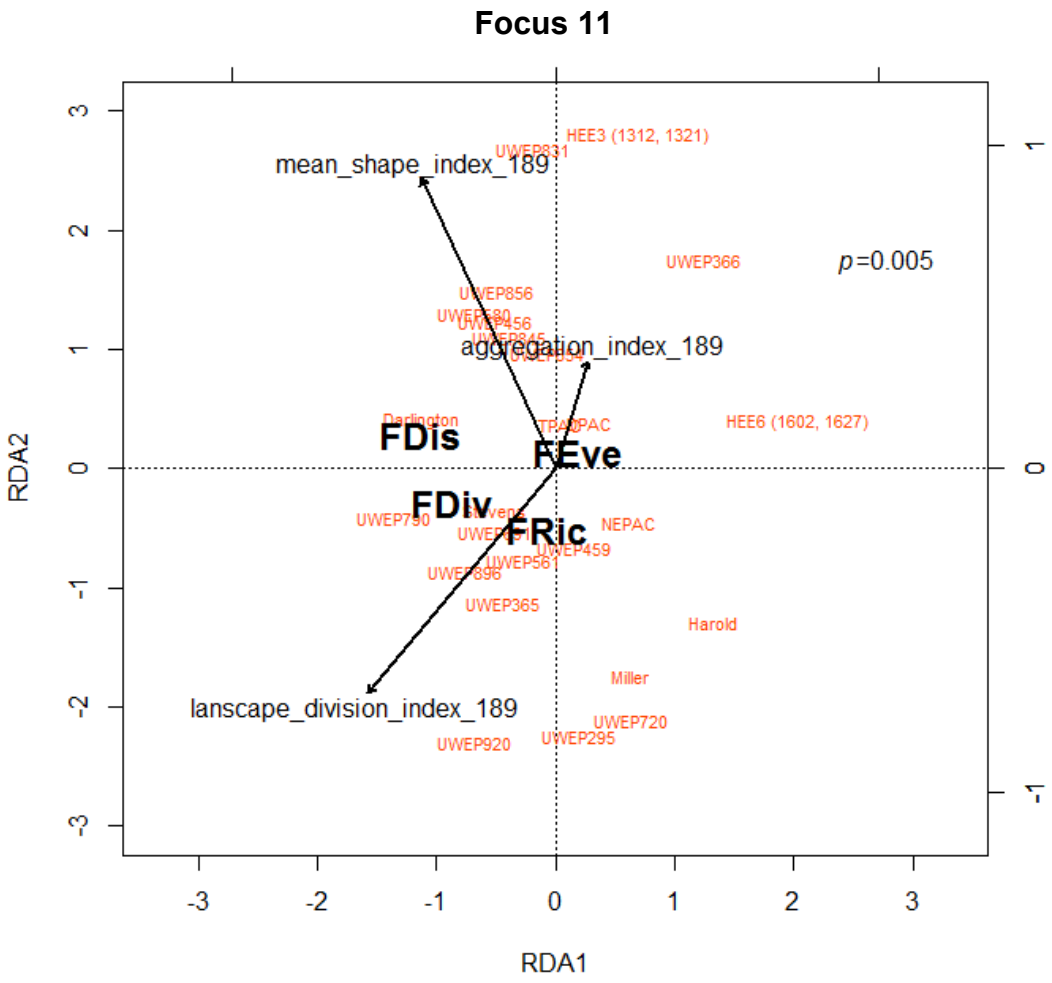

Figure K.5: Redundancy analysis (RDA) triplot at an analytical focus of 5.67 km (Focus 11). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

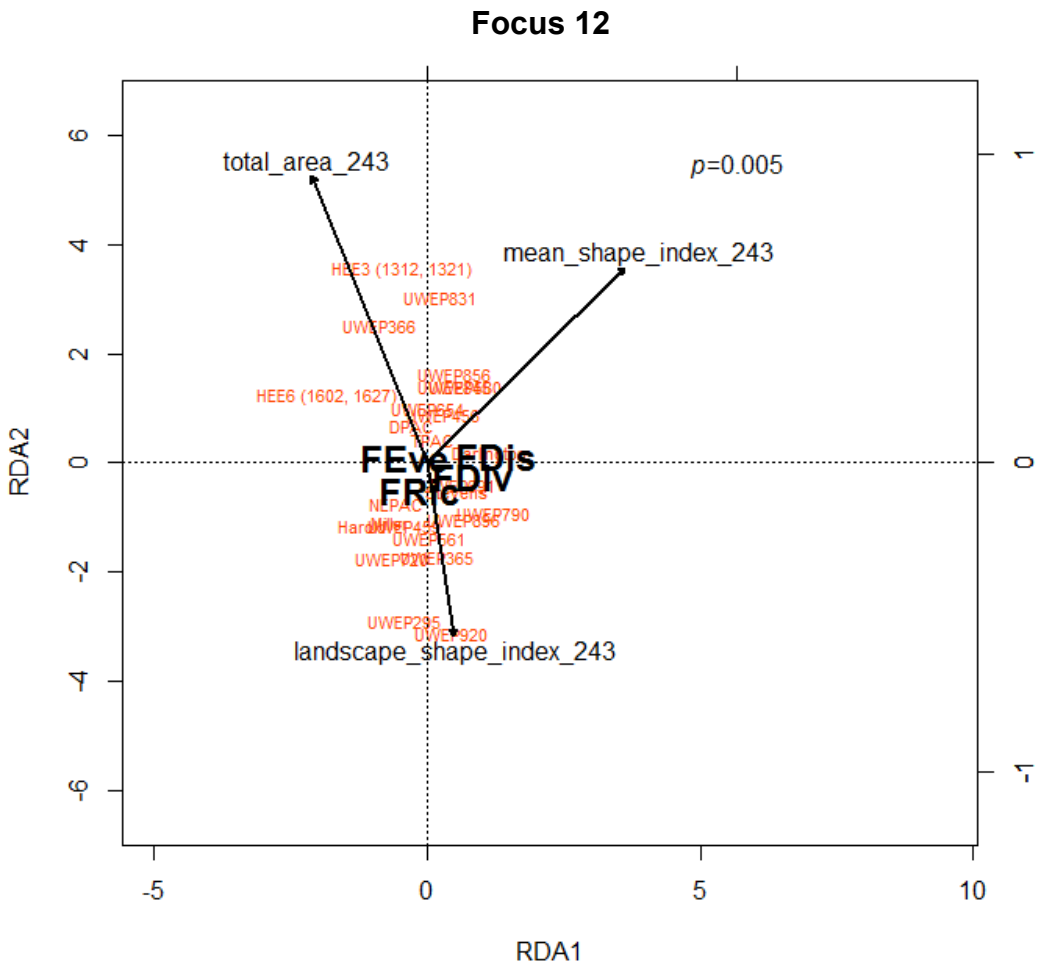

Figure K.6: Redundancy analysis (RDA) triplot at an analytical focus of 7.29 km (Focus 12). Response variables are functional diversity indices that measure functional trait space and how species abundance is dispersed within it. FDis = functional dispersion, FDiv = functional divergence, FEve = functional evenness, and FRic = functional richness.

Appendix L: Backgrounds used in chromatic and achromatic contrast calculations in Chapter 5

Table L.1: Backgrounds used in chromatic and achromatic contrast calculations in Chapter 5

Hymentopera	Region
Ancistrocerus adiabatus (de Saussure): solitary wasp that nests in borings in twigs, stems, and wood (Krombein et al. 1979)	gaster and pronotum
Camponotus chromaiodes Bolton: found in moist, decaying wood (Krombein et al. 1979)	gaster and pronotum
Formica exsectoides Forel: damages bark and cambium of small trees and shrubs (Krombein et. al. 1979)	gaster and pronotum
Polistes metricus Say: common paper wasp (Krombein et al. 1979)	gaster and pronotum
V. maculifons (Buysson): eusocial wasp common in hardwood forests (Akre et al. 1981)	gaster and pronotum
Forest	**Region**
Acer saccharum Marsh.	leaves, lichen, and moss on bark
Gleditsia triacanthos L.	bark

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Appendix M: Members of beetle visual contrast groups

UVS.1

Hololepta aequalis
Hololepta lucida
Platylomalus aequalis
Platysoma gracile
Platysoma leconti
Paromalus bistriatus

UVS.2

Aegomorphus modestus
Catogenus rufus
Gaurotes cyanipennis
Lepturges confluens
Neorthopleura thoracica
Platysoma aurelianum
Zenodosus sanguineus

UVS.3

Analeptura lineola	*Enoclerus nigripes*	*Neoclytus m. mucronatus*
Anelaphus villosus	*Eupogonius pauper*	*Neoclytus scutellaris*
Astyleiopus variegatus	*Graphisurus despectus*	*Obrium rufulum*
Astylidius parvus	*Graphisurus fasciatus*	*Orthosoma brunneum*
Astylopsis macula	*Heterachthes quadrimaculatus*	*Phymatodes amoenus*
Clytoleptus albofasciatus	*Leptostylus transversus*	*Psenocerus supernotatus*
Clytus ruricola	*Lepturges pictus*	*Pyticeroides laticollis*
Cucujus clavipes	*Madoniella dislocatus*	*Saperda imitans*
Cymatodera bicolor	*Metacmaeopes vittata*	*Strantalia luteicornis*
Cyrtophorus verrucosus	*Microgoes occulatus*	*Typocerus v. velutinus*
Dorcaschema cinereum	*Molorchus b. bimaculatus*	*Urgleptes querci*
Elaphidion mucronatum	*Neandra brunnea*	*Urgleptes signatus*
Elytramatatrix undata	*Neoclytus a. acuminatus*	*Xylotrechus colonus*

Figure M.1: Contrast groups using average avian UVS model in R package "pavo". Gray highlights = species retained in analysis.

VS.1

Cymatodera bicolor
Metacmaeopes vittata
Neandra brunnea
Neoclytus a. acuminatus
Neorthopleura thoracica
Pyticeroides laticollis

VS.3

Aegomorphus modestus
Catogenus rufus
Gaurotes cyanipennis
Platysoma aurelianum

VS.4

Hololepta aequalis
Hololepta lucida
Paromalus bistriatus
Platylomalus aequalis
Platysoma gracile
Platysoma leconti

VS.2

Analeptura lineola
Anelaphus villosus
Astyleiopus variegatus
Astylidius parvus
Astylopsis macula
Clytoleptus albofasciatus
Clytus ruricola
Cucujus clavipes
Cyrtophorus verrucosus
Dorcaschema cinereum
Elaphidion mucronatum
Elytramatatrix undata
Enoclerus nigripes
Eupogonius pauper
Graphisurus despectus
Graphisurus fasciatus
Heterachthes quadrimaculatus
Leptostylus transversus
Lepturges confluens
Lepturges pictus
Madoniella dislocatus
Microgoes occulatus
Molorchus b. bimaculatus
Neoclytus m. mucronatus
Neoclytus scutellaris
Obrium rufulum
Orthosoma brunneum
Phymatodes amoenus
Psenocerus supernotatus
Saperda imitans
Strangalia luteicornis
Typocerus v. velutinus
Urgleptes querci
Urgleptes signatus
Xylotrechus colonus
Zenodosus sanguineus

Figure M.2: Contrast groups (VS.1, VS.2, VS.3, and VS.4) using average avian VS model in R package "pavo". Gray highlights = species retained in analysis.

Appendix N: Members of avian assemblages.

Table N.1: Members of avian assemblages including scientific name, family, feeding guild and estimated cone type.

Avian Assemblage	Species	Scientific name	Family	Feeding guild	Cone type	Citation
VS.bark	Downy Woodpecker (DOWO)	*Coccyzus americanus*	Picidae	Bark	VS	Ödeen & Håstad (2013)
VS.bark	Hairy Woodpecker (HAWO)	*Picoides villosus*	Picidae	Bark	VS	Ödeen & Håstad (2013)
VS.bark	Pileated Woodpecker (PIWO)	*Dryocopus pileatus*	Picidae	Bark	VS	Ödeen & Håstad (2013)
VS.bark	Red-bellied Woodpecker (RBWO)	*Melanerpes carolinus*	Picidae	Bark	VS	Ödeen & Håstad (2013)
VS.bark	Red-headed Woodpecker (RHWO)	*Melanerpes erythrocephalus*	Picidae	Bark	VS	Ödeen & Håstad (2013)
VS.leaves	Yellow-Billed Cuckoo (YBCU)	*Coccyzus americanus*	Cuculidae	Leaves	VS	Aidala et al. (2012)

Table N.1: Members of avian assemblages including scientific name, family, feeding guild and estimated cone type, *continued*.

VS.flycatch	Acadian Flycatcher (ACFL)	*Empidonax virescens*	Tyrannidae	Flycatch	VS	Ödeen & Håstad (2003)
VS.flycatch	Eastern Phoebe (EAPH)	*Sayornis phoebe*	Tyrannidae	Flycatch	VS	Ödeen & Håstad (2003)
VS.flycatch	Eastern Wood-Pewee (EAWP)	*Contopus virens*	Tyrannidae	Flycatch	VS	Ödeen & Håstad (2003)
VS.flycatch	Great Crested Flycatcher (GCFL)	*Myiarchus crinitus*	Tyrannidae	Flycatch	VS	Ödeen & Håstad (2003)
UVS.bark	Carolina Wren (CARW)	*Thryothorus ludovicianus*	Troglodytidae	Bark	UVS	Ödeen et al. (2011)
UVS.bark	House Wren (HOWR)	*Troglodytes aedon*	Troglodytidae	Leaves and Bark	UVS	Ödeen et al. (2011)
UVS.bark	Tufted Titmouse (TUTI)	*Baeolophus bicolor*	Paridae	Bark	UVS	Ödeen & Håstad (2003)
UVS.bark	White-breasted Nuthatch (WBNU)	*Sitta carolinensis*	Sittidae	Bark	UVS	Ödeen et al. (2011)
UVS.bark	Yellow-Throated Warbler (YTWA)	*Setophaga dominica*	Parulidae	Bark	UVS	Ödeen et al. (2011)

Table N.1: Members of avian assemblages including scientific name, family, feeding guild and estimated cone type, *continued*.

Avian Assemblage	Species	Scientific name	Family	Feeding guild	Cone type	Citation
UVS.leaves	Baltimore Oriole (BAOR)	*Icterus galbula*	Icteridae	Leaves	UVS	Bennett & Cuthill (1994)
UVS.leaves	Blue-Gray Gnatcatcher (BGGN)	*Polioptila caerulea*	Sylviidae	Leaves	UVS	Ödeen & Håstad (2003)
UVS.leaves	Cerulean Warbler (CERW)	*Setophaga cerulea*	Parulidae	Leaves	UVS	Ödeen et al. (2011)
UVS.leaves	Gray Catbird (GRCA)	*Dumetella carolinensis*	Mimidae	Leaves	UVS	Bennett & Cuthill (1994)
UVS.leaves	Hooded Warbler (HOWA)	*Setophaga citrina*	Parulidae	Leaves	UVS	Ödeen et al. (2011)
UVS.leaves	House Wren (HOWR)	*Troglodytes aedon*	Troglodytidae	Leaves and Bark	UVS	Ödeen et al. (2011)
UVS.leaves	Kentucky Warbler (KEWA)	*Geothlypis formosa*	Parulidae	Leaves	UVS	Ödeen et al. (2011)

Table N.1: Members of avian assemblages including scientific name, family, feeding guild and estimated cone type, *continued*.

UVS.leaves	Orchard Oriole (OROR)	*Icterus spurius*	Icteridae	Leaves	UVS	Bennett & Cuthill (1994)
UVS.leaves	Rose-breasted Grosbeak (RBGR)	*Pheucticus ludovicianus*	Cardinalidae	Leaves	UVS	Bennett & Cuthill (1994)
UVS.leaves	Red-eyed Vireo (REVI)	*Vireo olivaceus*	Vireonidae	Leaves	UVS	Ödeen et al. (2011)
UVS.leaves	Scarlet Tanager (SCTA)	*Piranga olivacea*	Cardinalidae	Leaves	UVS	Bennett & Cuthill (1994)
UVS.leaves	Summer Tanager (SUTA)	*Piranga rubra*	Cardinalidae	Leaves	UVS	Bennett & Cuthill (1994)
UVS.leaves	Warbling Vireo (WAVI)	*Vireo gilvus*	Vireonidae	Leaves	UVS	Ödeen et al. (2011)
UVS.leaves	Worm-Eating Warbler (WEWA)	*Helmitheros vermivorum*	Parulidae	Leaves	UVS	Ödeen et al. (2011)
UVS.leaves	Yellow-Throated Vireo (YTVI)	*Vireo flavifrons*	Vireonidae	Leaves	UVS	Ödeen et al. (2011)

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Ödeen, A., O. Håstad, and P. Alström. 2011. Evolution of ultraviolet vision in the largest avian radiation-the passerines. BMC Evolutionary Biology 11: 313.

Ödeen, A. and O. Håstad. 2013. The phylogenetic distribution of ultraviolet sensitivity in birds. BMC Evolutionary Biology 13: 36.

Appendix O: Beetles collected among field sites (Chapter 5).

Table O.1: Beetles collected among field sites for Chapter 5. Removed species with <=5 total individuals among sites (in gray).

Aegomorphus modestus	*Clytus ruricola*	*Enaphalodes atomarius*
Analeptura lineola	*Cregya mixta*	*Enoclerus nigripes*
Anelaphus villosus	*Cregya oculata*	*Euderces picipes*
Astyleiopus variegatus	*Cucujus clavipes*	*Eupogonius pauper*
Astylidius parvus	*Cymatodera bicolor*	*Eupogonius pubescens*
Astylopsis macula	*Cymatodera inornata*	*Eupogonius subarmatus*
Astylopsis sexgutatta	*Cyrtophorus verrucosus*	*Gaurotes cyanipennis*
Bellamira scalaris	*Dorcaschema cinereum*	*Grammoptera rufipes*
Brachyleptura champlaini	*Dorcaschema nigrum*	*Graphisurus despectus*
Callimoxys s. sanguinicollis	*Eburia quadrigeminata*	*Graphisurus fasciatus*
Catogenus rufus	*Ecyrus d. dasycerus*	*Heterachthes quadrimaculatus*
Chariessa pilosa	*Elaphidion mucronatum*	*Hololepta aequalis*
Clytoleptus albofasciatus	*Elytramatatrix undata*	*Hololepta lucida*

Table O.1: Beetles collected among field sites for Chapter 5. Removed species with <=5 total individuals among sites (in gray), *continued*.

Hyperplatys aspersa	*Parelaphidion aspersum*	*Sphenostethus taslei*
Hyperplatys macula	*Parelaphidion incertum*	*Stenelytrana emarginata*
Leptostylus transversus	*Paromalus bistriatus*	*Stenocorus cinnamopterus*
Leptura plebeja	*Paromalus seminulum*	*Stenocorus schaumii*
Lepturges angulatus	*Phymatodes amoenus*	*Sternidius alpha*
Lepturges confluens	*Phymatodes lengi*	*Strangalepta abbreviata*
Lepturges pictus	*Phymatodes testaceous*	*Strangalia bicolor*
Lepturges symmetricus	*Placopterus thoracicus*	*Strangalia luteicornis*
Madoniella dislocatus	*Platylomalus aequalis*	*Strangalia solitaria*
Megacyllene caryae	*Platysoma aurelianum*	*Strophiona nitens*
Metacmaeopes vittata	*Platysoma gracile*	*Teretrius americanus*
Microgoes occulatus	*Platysoma leconti*	*Tessaropes tenuipes*
Molorchus b. bimaculatus	*Priocera castanea*	*Typocerus acuticauda*
Neandra brunnea	*Prionus laticolis*	*Typocerus deceptus*
Necydalis mellita	*Psenocerus supernotatus*	*Typocerus v. velutinus*
Neoclytus a. acuminatus	*Pyticeroides laticollis*	*Urgleptes querci*
Neoclytus m. mucronatus	*Saperda discoidea*	*Urgleptes signatus*
Neoclytus scutellaris	*Saperda imitans*	*Xylotrechus colonus*
Neorthopleura thoracica	*Saperda lateralis*	*Xylotrechus convergens*
Oberea praelonga	*Saperda tridentata*	*Zenodosus sanguineus*
Obrium rufulum	*Saperda vestita*	
Orthosoma brunneum	*Sarosesthes fulminans*	

Appendix P: Birds collected among field sites.

Table P.1: Birds collected among field sites. Removed species with <=10 total individuals among sites (in gray).

ACFL	CERW	HOWA	REVI
AMRE	CHSP	HOWR	RHWO
AMRO	CSWA	INBU	SCTA
BAOR	DOWO	KEWA	SUTA
BAWW	EAPH	NOCA	VEER
BCCH	EATO	NOFL	WAVI
BGGN	EAWP	OROR	WBNU
BLGR	TUTI	OVEN	WEWA
BLJA	GCFL	PIWO	WOTH
BTNW	GRCA	PROW	YBCU
CACH	GWWA	RBGR	YTVI
CARW	HAWO	RBWO	YTWA

VITA

VITA

Ashley L. Kissick

EDUCATION

Purdue University, Department of Entomology, West Lafayette, IN
Doctor of Philosophy, Entomology — Sept. 2010 – Dec. 2016

Maryville College, Maryville, TN
Bachelor of Arts, Biology, magna cum laude — Sept. 2003 – May 2007

LANGUAGES

Bilingual (English, Spanish)

RESEARCH/WORK EXPERIENCE

Research Associate, Research Advisor: Dr. Jeffrey D. Holland — Jan. 2012 – Dec. 2016
Purdue University, Department of Entomology, Ecological Sciences and Engineering Interdisciplinary Graduate Program

- Analyzed multivariate data and conducted all analyses in R
- Followed a multidisciplinary approach drawing from community ecology, landscape ecology, and ethology
- Developed theoretical approaches and expanded numerical analyses to examine community change and ecosystem stability after disturbance along environmental gradients
- Additional course experience: Geographic Information Systems (GIS), hydrology, soil science, plant mineral nutrition, and environmental policy
- Skilled in Microsoft Office, ArcGIS, analytical figure design in Inkscape and GIMP, ImageJ, Prezi

Research Associate, Research Advisor: Dr. Cliff Sadof Jan. 2011 – Dec. 2011
Purdue University, Department of Entomology, Ecological Sciences and Engineering Interdisciplinary Graduate Program

- Examined differences in arthropod feeding and pathogen damage on cut flowers grown under high tunnel versus field settings with the use of yellow sticky cards and visual inspections of plants

Undergraduate researcher, Research Advisor: Dr. Paul Threadgill June – Aug. 2006
Maryville College, Department of Biology

- Surveyed the movement of parasitoid wasps between coffee agroforestry systems, pasture, and forest with Malaise traps at CATIE, Turrialba, Costa Rica
- Analytical tools (most transferable): histology for TEM and light microscopy, PCR

Academic Coordinator May – July 2010
EARTH University, Office of International Academic Relations, Guácimo, Costa Rica

- Provided Spanish-English interpretations in the field for guided group tours and a visiting ethnobotany scholar researching the culinary use of a tropical tree *Cnidoscolus aconitifolius* "chicasquil" and medicinal use of plants by rural subsistence farmers in Costa Rica
- Prepared logistics for and guided travel tours throughout Costa Rica for international university and professional groups
- Developed itineraries and interactive learning assessments for international student programs hosted by the University

TEACHING EXPERIENCE
Teaching Assistant, AGRY 320 "Genetics" June 2014 – June 2016
Purdue University, Department of Agronomy

- Guest lectured 2 – 3 classes/semester, class size ranged from 25 – 215 students; topics included molecular, Mendelian, population, and quantitative genetics, large scale chromosome changes, genetic control of embryo development, gene regulation in prokaryotes and eukaryotes
- Wrote exams, quizzes, and homework sets including the design of new questions and graded these assessments
- Explained course topics to students during weekly office hours
- Organized and led review and help sessions (ex: 2/wk during summer terms)

Written evaluation comments:

- *"…knowledgeable and has an in-depth understanding during lectures. Adding in little jokes or memes to the lecture helps to relate and capture the interest of students."*
- *"…did a good job especially in trying to make material more interactive and interesting."*
- *"Ashley was very approachable throughout the course. She always seemed very organized and returned our tests/quizzes/homeworks back to us in a timely manner. The lectures she taught were very informational, and I thoroughly enjoyed learning from her."*

Graduate Teaching Certificate Sept. 2016
Purdue University, Center for Instructional Excellence, West Lafayette, IN

RESEARCH PUBLICATIONS

Kissick, A. L., J. B. Dunning, and J. D. Holland. 2016. New approaches for examining changes in functional diversity across trophic levels and environmental gradients. (in prep).

Kissick, A. L. and J. D. Holland. 2016. Ecological stabilizing mechanisms: a test using expanded methodology for detection within functional groups. (in prep).

Kissick, A. L., E. Fernández-Juricic, J. B. Dunning, J. D. Holland, and P. Baumhardt. 2016. Linking predator and prey: foraging strategies and visual contrasts are important for birds with violet-sensitive vision. (in prep).

CONFERENCE PRESENTATIONS

Kissick, A. L. and J. D. Holland. Beetle functional diversity responds at different spatial foci. 2016 Annual Meeting of the US Regional Association of the International Association for Landscape Ecology, Ashville, NC, USA, April 5, 2016.

Holland, J.D. and **A. L. Kissick**. Novel functional diversity traits of insect communities. 131st Annual Indiana Academy of Science Meeting, Indianapolis, IN, USA, March 26, 2016.

Kissick, A. L. and J. D. Holland. Stability mechanisms in beetle functional groups. 131st Annual Indiana Academy of Science Meeting, Indianapolis, IN, USA, March 26, 2016.

Kissick, A. L. and J. D. Holland. Hardwood Ecosystem Experiment harbors greater functional diversity of longhorned beetles and their generalist predators. 130th Annual Indiana Academy of Science Meeting, Indianapolis, IN, USA, March 21, 2015.

Kissick, A. L. and J. D. Holland. Functional groups affected differently by disturbance and landscape. 99th Ecological Society of America Annual Meeting, Sacramento, CA, USA, August 15, 2014.

Kissick, A. L. and J. D. Holland. Predators go the distance. 129th Annual Indiana Academy of Science Meeting, Indianapolis, IN, USA, March 15, 2014.

RESEARCH POSTERS

Kissick, A. L. and J. D. Holland. Beetle functional diversity response to habitat fragmentation. Poster presented at the Ecological Science and Engineering Interdisciplinary Graduate Program Symposium, West Lafayette, IN, USA, October 20, 2014.

Kissick, A. L. and J. D. Holland. Predator and prey response to disturbance and landscape. Poster presented at the Office of Interdisciplinary Graduate Programs Spring Reception, West Lafayette, IN, USA, April 2, 2014.

Kissick, A. L. and J. D. Holland. Exploring the diversity of beetle predators in Indiana hardwood forests. Poster presented at the Office of Interdisciplinary Graduate Programs Spring Reception, Purdue University, April 1, 2013.

Kissick, A. L. and J. D. Holland. A Survey of beetle predators along a landscape gradient. Poster presented at the Ecological Sciences and Engineering Symposium, Purdue University, October 16-17, 2012.

Kissick, A. L., C. Sadof, and R. Lopez. Seasonal phenologies of pests in Indiana Cut Flower Farms. Poster presented at the Entomological Society of America national meeting, Reno NV, USA, November 13-16, 2011.

PROFESSIONAL AFFILIATIONS

- Ecological Society of America
- Entomological Society of America
- Indiana Academy of Sciences
- International Association for Landscape Ecology

AWARDS AND HONORS

Purdue University

Bilsland Dissertation Fellowship	2016
Andrews and Blosser Environmental Travel Grant	2014
People's Choice Award, ESE IGP Symposium Poster competition	2014
Research Assistantship, Purdue University Graduate School	2013 – 2014
USDA Agro□Ecosystem Services (AES) National Needs Fellowship	2010 – 2013
NSF Graduate Research Fellowship Honorable Mention	2012
ESE Symposium poster presentation	2010
NSF Graduate Research Fellowship Honorable Mention	2010
Big Ten+ Graduate School Expo Travel Scholarship	2009

Maryville College

Dean's Scholar	2003 – 2007
Alpha Gamma Sigma Honors Society	2007
Randolph Shields Award	2007
Liberal Arts Award	2007
Eli Lilly Summer Internship Grant	2006
Susan Allen Green Award	2006
Outstanding Performance in Structural Chemistry	2005
Southern Africa Travel Scholarship	2005

COMMUNITY AND PROFESSIONAL SERVICE

Illustrations

Purdue University

2016

- Thumbnail image for: Long, E. Y. and C. H. Krupke. 2016. Non-cultivated plants present a season-long route of pesticide exposure for honey bees. *Nature Communications* 7: 11629.
- Diagram to illustrate the differences between two-stage and traditional agricultural ditch designs included in: Speelman, J. 2016. Zoobenthic Assemblages, Environmental Drivers, and Bioindicators in Agricultural Drainage Ditches. PhD thesis, Purdue University, Dissertation, West Lafayette, IN.
- Sketches and final images for a video game cabinet to house games for entomology education and outreach Dec. 2014 – Sept. 2016

Maryville College

- Tadpole mouthparts 2005
  - A series of illustrations demonstrating differences in juvenile development in the labial tooth rows and oral disc in *Rana silvatica* for the research of Dr. W. B. Cash
- Dissection microscope diagram 2005
  - Included in a laboratory manual used in a freshmen biology class

NASAR, the National Association of Search and Rescue

- Official NASAR K9 patch design 2005

***A Natural Bent,* Scott, R.**

- Book cover illustration for published poetry book by a Maryville, TN author 2004

Purdue University, Ecological Sciences and Engineering (ESE) Interdisciplinary Graduate Program

ESE Symposium Fundraising Committee member 2011

- Worked as part of a committee to raise over $6,000 through local business donations to fund the annual ESE Symposium held at Purdue University

Purdue University, Department of Entomology

Bug Bowl volunteer (annual outreach education event) 2011 – 2016

- Insect Observation Room and Animal Barn docent
- Face painting and arts and crafts

Research team member, Bioblitz and citizen science projects

- Assessed the forest beetle biodiversity in these areas by setting arrays of traps to capture beetles, curating the insects and identifying them to species. The species list was included in a final report given to land managers.
  - Urban parks in Indianapolis, IN Academy of Science Bioblitz 2016
  - Eagle Marsh Nature Preserve, IN Acadamy of Science Bioblitz 2014
  - Brown County Ecoblitz 2014
  - Kankakee Sands, IN Acadamy of Science Bioblitz 2012

- Collected water samples in the Wabash River Watershed to be destined for water quality testing
  - Wabash River Sampling Blitz 2013
  - Wabash River Sampling Blitz 2011

Winter owl survey volunteer, Hardwood Ecosystem Experiment (HEE) 2010 – 2014

- Surveyed screech owls and barred owls along bird points in the HEE as part of a community outreach program